COOPERATION AND COMPETITION IN PAPER WASP AND HUMAN SOCIETIES

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In this dissertation, I combine theoretical and empirical approaches, as well as concepts from the human and non-human animal literature, to investigate the effect of different types of competition on cooperation among members of a social group. These lines of research are complementary and mutually reinforcing: drawing on approaches developed to analyze the behavior of one taxon to investigate another can help us elucidate universal principles governing the evolution of cooperation and conflict over resource division.

In chapters 1 and 2, I apply game theoretic "tug-of-war" models of reproductive skew to conflict over resource contribution and division within human groups. In chapter 1, I consider competition over individuals' personal resources. The results of a laboratory economic game support the theoretical prediction that the potential for such competition favors cooperative contribution to an equally shared group resource from which everyone benefits. In chapter 2, I relax the assumption of equal sharing, and demonstrate theoretically and empirically that competition over resource division leads to lower contributions and payoffs.

In chapters 3 and 4, I extend a tug-of-war model of intergroup competition to investigate conflict over resources shared among social insect colonies. I focus on the primitively eusocial wasp *Polistes dominulus*, as individuals display behavioral flexibility and benefit from investing in

both cooperation and conflict. In chapter 3, I use field and lab experiments test theoretical predictions that *P. dominulus* may not face a simple tradeoff between within-group cooperation and competition. In chapter 4, I demonstrate mathematically that asymmetries among group members in relatedness and dominance affect cooperation and conflict within insect societies engaged in intergroup competition.

In chapter 5, I consider competition over foraging contributions in *P. dominulus*, and show in a field manipulation that aggression towards experimentally removed workers is higher when these wasps received food while they were in the lab. This leads to questions about the possible function of aggression in within-group competition and cooperation in this species.

BIOGRAPHICAL SKETCH

Jessica Livia Barker grew up in London, where she divided her childhood between Regent's Park Zoo and Hampstead Heath. This prepared her well to read Natural Sciences (Zoology) at the College of the Blessed Virgin Mary, St John the Evangelist, and the Glorious Virgin St Radegund, near Cambridge. Her post-graduation year of extracting DNA from *Polistes* legs and playing CDs to blue monkeys solidified Jessica's interest in behavioral ecology, so in 2006 she moved to Ithaca with two suitcases and a pot of Marmite, and began her PhD at Cornell. She has subsequently become acquainted with the local wasps and WASPs, and has completed triathlons on six of the Finger Lakes. People still ask her whether she is Australian.

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Finally, thanks to my parents, Nancy Pistrang and Chris Barker, and sister, Anna Barker, for bearing the costs of their relative's dispersal; to my grandparents, Joe and Judy Pistrang, for embracing the benefits; and to Caitlin Stern, for being the best officemate I could wish for.

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CHAPTER 1

COMPETITION OVER PERSONAL RESOURCES FAVORS CONTRIBUTION TO SHARED RESOURCES IN HUMAN GROUPS

Jessica L. Barker, Pat Barclay and H. Kern Reeve

Members of social groups face a trade-off between keeping personal resources for themselves and cooperatively contributing them to produce a shared group resource. Many group resources are shared equitably: they may be intrinsically non-excludable public goods, such as vigilance against predators; or so large that there is little cost to sharing, such as cooperatively hunted big game. However, group members' personal resources, such as food hunted individually, may be monopolizable. In such cases, an individual may benefit by investing in taking others' personal resources, and in defending one's own resources against others. We use a game theoretic "tug-of-war" model to predict that when such competition over personal resources is possible, players will contribute more towards a group resource, and also obtain higher payoffs from doing so. We test and support these predictions in two laboratory economic games in humans, comparing people's investment decisions in games with and without the options to compete over personal resources or invest in a group resource. Our results help explain why people cooperatively contribute to group resources, suggest how a tragedy of the commons may be avoided, and highlight unifying features in the evolution of cooperation and competition in human and non-human societies.

INTRODUCTION

Conflict over the division of resources arises across the animal kingdom, from intraorganismal conflict (Michod and Roze 2001) to competition among social group members (Keller and Reeve 1994; Sherman et al. 1995; Dugatkin 1997), including humans (Mace and Alvergne 2012). For individuals in social groups, two types of resources can potentially be divided: personal resources that each individual has kept for itself, such as food from a solitary hunt, and group resources consisting of individuals' pooled contributions, such as large prey caught in a cooperative hunt, and which are shared, often equally, among all group members (Stanford and Bunn 2001; Gurven 2004). In this study, we investigate how the potential to take other people's personal resources may increase the benefit of contributing to group resources that are equitably divided, a topic of considerable social and political importance in human groups (Wilkinson and Pickett 2007).

Some resources to which group members contribute (hereafter, group resources) are non-excludable and non-rivalrous (public goods, *sensu strictu*): that is, they are intrinsically accessible to all group members, are non-depletable, and thus there is no competition over their division. For example, in an insect society, workers' investments in raising the queen's offspring benefits all group members according to their relatedness to the queen (Hamilton 1964); likewise, the benefits of predator inspection or vigilance (e.g. in guppies: Dugatkin 1991) are automatically shared. Similarly, many group resources shared by humans are intrinsically non-contestable public goods, such as clean air, public radio, and defense against other groups (Boone 1992).

Other group resources are depletable or potentially monopolizable, for example food shared among chimpanzees *Pan troglodytes* (Melis et al. 2006) and humans (Bliege Bird and Bird 1997). However, in practice many of these resources are shared, such that they are functionally non-contestable. Sharing may occur because the group resource is so large, e.g. big game from a cooperative hunt or plentiful fish stocks, that it is too costly monopolize (i.e. not economically defendable: Boone 1992; Cashdan 1992), or that sharing is low-cost if an individual becomes satiated (i.e. tolerated theft: Blurton Jones 1984; Blurton Jones 1987; Winterhalder 1996b). Alternatively, group members may benefit by investing in mechanisms to prevent competition over shared resources, such as policing (Ratnieks and Reeve 1992; Frank 1995; Flack et al. 2006; Ratnieks and Wenseleers 2007; El Mouden et al. 2010) and, in human groups, social institutions (Bowles et al. 2003; West et al. 2011). Indeed, human groups are noteworthy for the degree to which potentially monopolizable group resources are shared equally (Kaplan and Hill 1985; Hawkes et al. 2001).

In contrast, individuals may keep personal resources for themselves, which are often excludable, depletable "private goods", such as wealth or food (Boone 1992), for example the !Kung own small prey from individual hunts (Hawkes 2001). In some societies, there is less emphasis on sharing goods and more on keeping personal resources for oneself, e.g. among the Machiguenga (Henrich et al. 2005), and in these cases, an individual may be able to increase the size of her own personal resources by selfishly taking personal resources from others. For example, in non-human primates, harassment over food is common, e.g. in macaques *Macaca fascicularis* (Kummer and Cords 1991), squirrel monkeys *Saimiri boliviensis* (Stevens 2004) and chimpanzees *Pan troglodytes* (Goodall 1986); and members of some human societies similarly

attempt to steal others' personal resources, e.g. among the Dobu (Benedict 1934) and the Mikea (Tucker 2004). In response, individuals benefit by investing in resource defense (Chapman and Kramer 1996) in order to reduce their group-mates' selfish efforts. For example, hymenopteran workers eat eggs selfishly laid by other workers in order to lay their own (Bonckaert et al. 2010); humans also invest in policing to protect their resources.

Investing in taking others' and defending one's own resources (hereafter, "competition") is costly to all group members, constituting an "arms race" of investment in manipulation and counter-manipulation that reduces the amount that individuals invest in their personal or group resources (Ratnieks and Reeve 1992). There is thus a trade-off between investing in group resources, personal resources, and competition, and so the division of contestable personal resources may affect individuals' investments in group resources. We hypothesize that competition over individuals' personal resources increases the benefit of contributing to a non-contested group resource of which all group members obtain an equitable share: this is because an individual will reliably gain a benefit from greater investment in the group resource, but any benefit from greater investment in personal resources may be reduced by others' investments in competition. Under this hypothesis, we predict that: (1) given that individuals have the opportunity to contribute to a group resource, contributions will be higher when competition over personal resources is possible versus when it is prevented; and (2) given that there is competition over personal resources, individuals' payoffs will be higher when they have the opportunity to contribute to a group resource.

We investigated this hypothesis both mathematically and empirically. Firstly, we used a game theoretic "tug-of-war" model (Reeve et al. 1998) to predict individuals' optimal investments in cooperation and competition. In a basic tug-of-war, an individual obtains a fraction of resource proportional to its investment in competition relative to other group members. Individuals' investments in competition diminish the absolute amount of the contested resource, i.e. there is a tradeoff between increasing one's own fraction and reducing the total amount of resource. Tugs-of-war have been used to analyze the division of group resources in both invertebrates, particularly social insects (Reeve and Keller 2001), and vertebrates, e.g. mountain gorillas *Gorilla beringei beringei* (Bradley et al. 2005), cooperatively breeding cichlids *Neolamprologus pulcher* (Heg and Hamilton 2008) and humans (Barclay 2011; Barker et al. 2012). Here, we apply the tug-of-war framework to the division of personal resources. Secondly, we tested the verbal and mathematical predictions in human groups. We used laboratory economic games based on a "public goods" game (Dawes and Thaler 1988; Davis and Holt 1993; Ledyard 1995): economic experiments do reflect people's behavior outside the laboratory (Henrich et al. 2005) and provide a rigorous way to investigate the collective action problem of resource sharing faced by pre-industrial human groups.

MODEL

No competition over personal resources

We start by considering a classic public goods game (Dawes and Thaler 1988; Davis and Holt 1993; Ledyard 1995) where each individual has a personal resource of value *v*, of which she contributes an amount *y* to a shared group resource, and keeps *v*-*y* for herself. All contributions to the group resource are summed and multiplied by *k*, and then split equally among the *n* members of the group.

We seek the optimal contribution *y** that maximizes the amount of resources an individual obtains, i.e. maximizes its fitness. To do this, we consider the amount of resources w_y obtained by a focal individual contributing *y* in a population of *n*-1 other individuals contributing *y**:

Equation 1.1

$$w_y = (v - y) + \frac{1}{n}k(y + (n-1)y^*)$$

At the Nash equilibrium, the focal individual's contribution *y* is equal to all others' contributions *y**, and $dw_y/dy = 0$, which allows us to solve for *y**. We find that *y** is an endpoint maximum: that is, individuals should contribute either all (*v*) or none (0) of their personal resources, but not an intermediate amount. (For details on finding the endpoint maxima, see appendix.) We determine that when $k>n$, $y^* = v$ (individuals maximize their fitness by contributing all of their personal resources, and obtain a payoff $w_y=kv$), but when $k<n$, $y^* = 0$ (individuals maximize their

fitness by keeping all of their own resources, and obtain a payoff $w_y=v$). This basic finding replicates previous theoretical work on public goods contributions (e.g. Davis and Holt 1993; Ledyard 1995), and we build on it in subsequent sections.

"Tug-of-war" over personal resources

We now consider the case where any personal resource that an individual does not contribute to the shared group resource may be taken by other group members. An individual invests *x* in attempting to defend her personal resources from others, and *z* in trying to take others' personal resources; i.e., a "tug-of-war" competition (Reeve et al. 1998) over resources not contributed to the group. Each investment *z* is spread evenly among the other group members; that is, an investment *z* is corresponds to an investment $\frac{z}{(n-1)}$ in taking from any given player. The effectiveness of a given investment in resource defense relative to an investment in taking from others is given by the factor *b*.

We seek the optimal values *x**, *y** and *z**, and again do so by considering a mutant individual adopting the strategies *x*, *y* and *z*, in a population of *n*-1 others adopting the optimal strategies *x**, *y** and *z**. The fraction of resources that the focal individual defends, *d*, is determined by her investment in resource defense relative to the other players' investments in taking from her:

Equation 1.2

$$d = \frac{bx}{bx + (n-1)\frac{z^*}{(n-1)}}$$

The fraction of resources that the focal individual takes from another player, *t*, corresponds to her investment in taking from that player relative to that player's resource defense and *n*-2 other players' efforts in taking from him:

Equation 1.3

$$t = \frac{\frac{z}{(n-1)}}{\frac{z}{(n-1)} + bx^* + (n-2)\frac{z^*}{(n-1)}}$$

After her investments above, the focal player has an amount *v*-*x*-*y*-*z* of resources to keep for herself. The total amount of resources that this focal individual obtains, w_{xyz}, is therefore a fraction *d* of what she kept for herself plus a fraction *t* of what each other player kept for himself, plus an equal share of the contributions to the group resource:

Equation 1.4

$$w_{xyz} = d(v - x - y - z) + (n-1)t(v - x^* - y^* - z^*) + \frac{1}{n}k(y + (n-1)y^*)$$

We then find the partial derivatives $\delta w_{xyz}/\delta x$, $\delta w_{xyz}/\delta y$ and $\delta w_{xyz}/\delta z$; we evaluate these derivatives at $x=x^*$, $y=y^*$ and $z=z^*$, when all individuals are adopting the optimal strategies, and set them equal to zero. As above, we find an endpoint maximum for y^*: when $k>1$, $y^*=v$ (individuals should contribute everything, and obtain a payoff $w_{xyz}=kv$), and when $k<1$, $y^*=0$ (individuals should contribute nothing). Thus, the condition favoring contributions to the group resource in this game with a tug-of-war over personal resources ($k>1$) is more permissive than that in the standard public goods game with no tug-of-war ($k>n$).

For cases where y*=0 (including when there is simply no group resource to which players can contribute), we simultaneously solve $\delta w_{xyz}/\delta x=0$ and $\delta w_{xyz}/\delta z=0$ for the values x^* and z^*. We verify that these correspond to fitness maxima by checking that the second derivatives are negative. When resistance and stealing are equally effective ($b=1$, as in our experiment; see appendix for solutions when $b\neq1$), we find that the optimal strategies are:

Equation 1.5

$$x^* = \frac{(n-1)v}{n^2}, \qquad z^* = \frac{(n-1)^2 v}{n^2}$$

Thus, a player should invest n-1 times as much in taking (z^*) than in defense (x^*), since each investment in taking is spread among the n-1 other players.

Substituting these values for x^* and z^* into w_{xyz}, we find that at equilibrium an individual obtains a payoff $w_{xyz}=\frac{v}{n}$. Because this payoff is smaller than kv, players do better by investing in the group resource whenever one is available and there are collective gains from doing so ($k>1$).

METHODS

Overview of economic game

We recruited participants from the Cornell University community using posters and mailing lists. Participants played an economic game in groups of four people (118 females and 66 males of

various ethnicities, mean age: 20.85 years ±s.e 0.30 years). Each group (*n*=46) of participants played two experimental conditions (see below), programmed using z-Tree software (Fischbacher 2007). Each participant played the game at a computer terminal visually isolated from the other players; all decisions were confidential, and methods were approved by the Institutional Review Board for Human Participants.

Players completed instructions and a test of understanding before starting each experimental condition in the game. Each condition contained 10 rounds; players received 100 "lab dollars" (L$) each round, which they could invest in different ways depending on the condition. Participants did not know how many rounds of the game they would play. At the end of the game, lab dollars were exchanged for cash payoffs in US dollars (L$300:US$1, plus a baseline payment of US$2), with a mean payoff of US$9.10 ± s.e. US$0.18, with exact earnings depending on participants' decisions during the game.

Public goods game condition: Contribute & Keep (CK)

Each participant could divide her money among two options: contribution to the group (C) and setting aside personal money to keep for herself (K). (In the experiment, these were called the "group fund" and "production fund" respectively, to avoid framing problems). As in a standard public goods game, contributions to the group fund were doubled and redistributed equally among all players (Davis and Holt 1993; Ledyard 1995; Barclay 2004). Each player's payoff at the end of each round was therefore equal to the money she kept plus her quarter share of the

doubled group fund (Equation 1.1). Information about all players' contributions and payoffs was displayed on each participant's computer screen before she moved onto the next round.

Tug-of-war condition: Keep, Take, & Defend (KTD)

In this condition, a group fund was not available for players to contribute to. Each participant could keep money for herself (K), but could also invest in attempting to take the personal money that others kept (T) and defending her own personal money from others' attempts to take it (D). These investments constitute a "tug-of-war" over players' personal resources, corresponding to strategies *z* and *x* respectively in the model (see above); in the experiment they were called "extraction" and "retention". Each player's payoff at the end of each round was equal to the personal money she defended plus the money she took from others (i.e. Equation 1.4 with $y=y^*=0$). As in the Contribute & Keep condition (CK), participants saw a computer screen with all players' investments in each fund and their payoffs before they started a new round of the game.

Of the money kept for herself, the amount that a participant retained at the end of the round depended on her investment in defense relative to other players' investments in taking from her (Equation 1.2). For example, if player A invested L$30 in defense and the other three players invested a total of L$50 in taking from her, then A would end up with a 3/8 share [30/(30+50)] of her own personal money.

As in the model above, a player's investment in taking from others was divided among the three other group members: for example, a L$30 investment meant a player invested L$10 in taking from each other player's personal money. The amount of money that a participant received from another player's personal keepings depended on her own investment in taking from him relative to his investment in defense, and the other players' investments in taking (Equation 1.3). For example, if player B invested L$30 in defense, player A invested L$10 in taking from him, and the other two players invested L$20 each in taking from him, player A would get a 1/8 share (10/[10+30+20+20]) of B's personal money. If no-one invested in taking from anyone else, each person would keep all of her personal money.

Public goods game plus tug-of-war condition: Contribute, Keep, Take, & Defend (CKTD)

Participants playing this condition had four options. Each player could invest in keeping money (K) for herself; taking (T) from others' kept amounts; and defending (D) her own kept amount from others' taking, as in the tug-of-war game. Additionally, each player could invest in contributing (C) to a group fund that was doubled and divided equally, as in the public goods game. That is, investments in taking and defending apply only to the money players kept for themselves, and not to the money contributed to the group fund. Each participant's payoff at the end of each round was thus equal to one quarter of the doubled group fund, plus personal money she defended, plus others' personal money that she took (Equation 1.4).

Comparisons of experimental conditions and statistical analyses

Each group played two experimental conditions, with the order of conditions counterbalanced between groups. This allowed us to make the following comparisons:

Comparison 1: CKTD versus CK (i.e. public goods game with/without tug-of-war). 26 groups played experimental conditions CK and CKTD; that is, the possibility to invest in the tug-of-war differed between conditions.

Comparison 2: CKTD versus KTD (i.e. tug-of-war with/without group resource). 20 groups played experimental conditions KTD and CKTD; that is, the possibility to contribute to the shared group fund differed between conditions.

The within-subject design is an important feature of this empirical test. The model predicts that since n=4 and k=2 in our game: a) in the CKTD condition, participants should contribute everything ($y^*=v$); b) in the CK condition, participants should keep all of their personal resources ($y^*=0$); and c) in the KTD condition, participants should adopt the stable intermediate values of x^* and z^* (Equation 1.5). However, people typically avoid extreme decisions in laboratory economic games (Kümmerli et al. 2010), even when doing so is not optimal, and thus are unlikely to invest the absolute values predicted by any model (Ledyard 1995; Yamagishi et al. 2009). The relevant predictions here are therefore the relative differences in people's decisions between experimental conditions (Kümmerli et al. 2010; Barker et al. 2012).

We treated each group of 4 participants as an *n* of 1, to control for interdependence within groups. We analyzed the data using a general linear model (SPSS 17.0) with experimental condition and round as within-groups variables, and with the order of conditions as a between-groups variable. For two groups in the CKTD versus CK experiment, minor problems arose with the instructions program during the game (quiz questions appearing at the wrong time or not at all), but excluding these groups from the analysis did not affect the results.

RESULTS

Comparison 1: CKTD versus CK (with/without tug-of-war).

Contributions to the group fund were significantly higher when people could invest in the tug-of-war (CKTD condition: L$53.4 ± s.e. L$4.3) than in the condition without a tug-of-war (CK condition: L$39.0 ± s.e. L$4.6; $F(1,24)=10.86$, $p=0.003$). This is all the more striking given that participants had the opportunity to spread their money among four options in the CKTD condition, compared with two in the CK condition: having more options would normally dilute participants' investments among those options, and yet participants still invested more in the group fund, and kept less money for themselves, when the tug-of-war was present (see appendix for further evidence of this).

There was a significant interaction between experimental condition and round number ($F(9,216)=10.20$, $p<0.001$): in the CK condition, contributions fell over time ($F(9,216)=10.12$,

$p<0.001$), whereas contributions increased in the CKTD condition ($F(9,216)=3.04$, p=0.002). The possibility of investing in a tug-of-war thus means that contributions do not fall (Figure 1.1). Order was counterbalanced across sections; see appendix for an analysis of order effects on contributions over time.

Despite the higher contributions in the CKTD condition, participants earned significantly higher payoffs in the CK condition (L$139.0 ±L$4.6) compared to the CKTD condition (L$121.1 ±L$7.0; $F(1,24)=8.85$, $p=0.007$, no effect of order; Figure 1.2a); that is, people were worse off when they had the option to invest in a tug-of-war, because the tug-of-war used up resources.

Comparison 2: CKTD versus KTD (with/without group resource)

Participants' payoffs were significantly higher when they could contribute to a shared group resource (CKTD condition: L$123.6 ± s.e. L$9.6) than in the experimental condition without the option for contribution (KTD condition: L$28.6 ± s.e. L$1.4; $F(1,18)=90.77$, $p<0.001$; Figure 1.2b). There was no effect of order or interaction with order on any of the results regarding participants' payoffs (all Fs <1).

People's higher payoffs in the CKTD condition may simply be because money contributed to the group fund, unlike that kept in a personal fund, was not subject to the tug-of-war, or because it was doubled before being equally divided among participants ($k=2$). In order to distinguish between these alternatives, we can hypothetically adjust people's payoffs to determine what they would have obtained if the group resource had not been doubled ($k=1$). Participants' adjusted

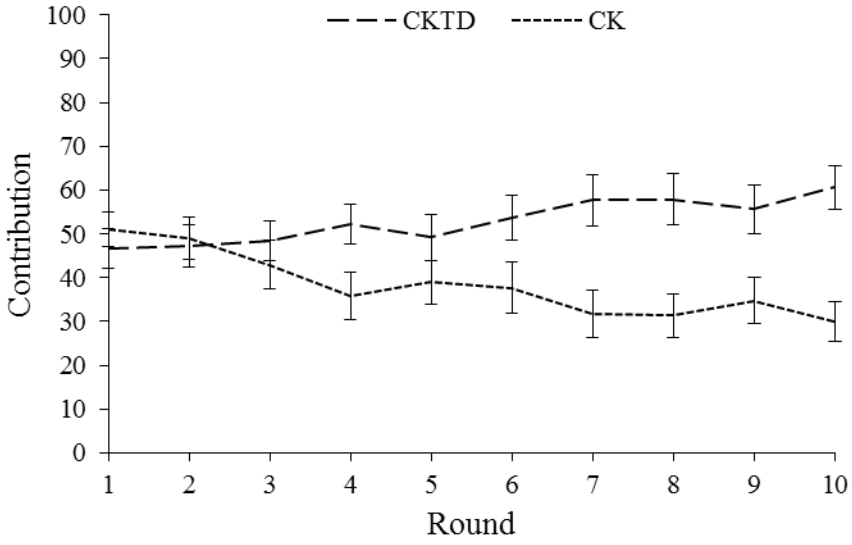

Figure 1.1. Mean (± s.e.) contributions in lab dollars to the group fund in each round when there is a public goods game plus tug-of-war (CKTD condition, dashed line) versus a public goods game only (CK condition, dotted line).

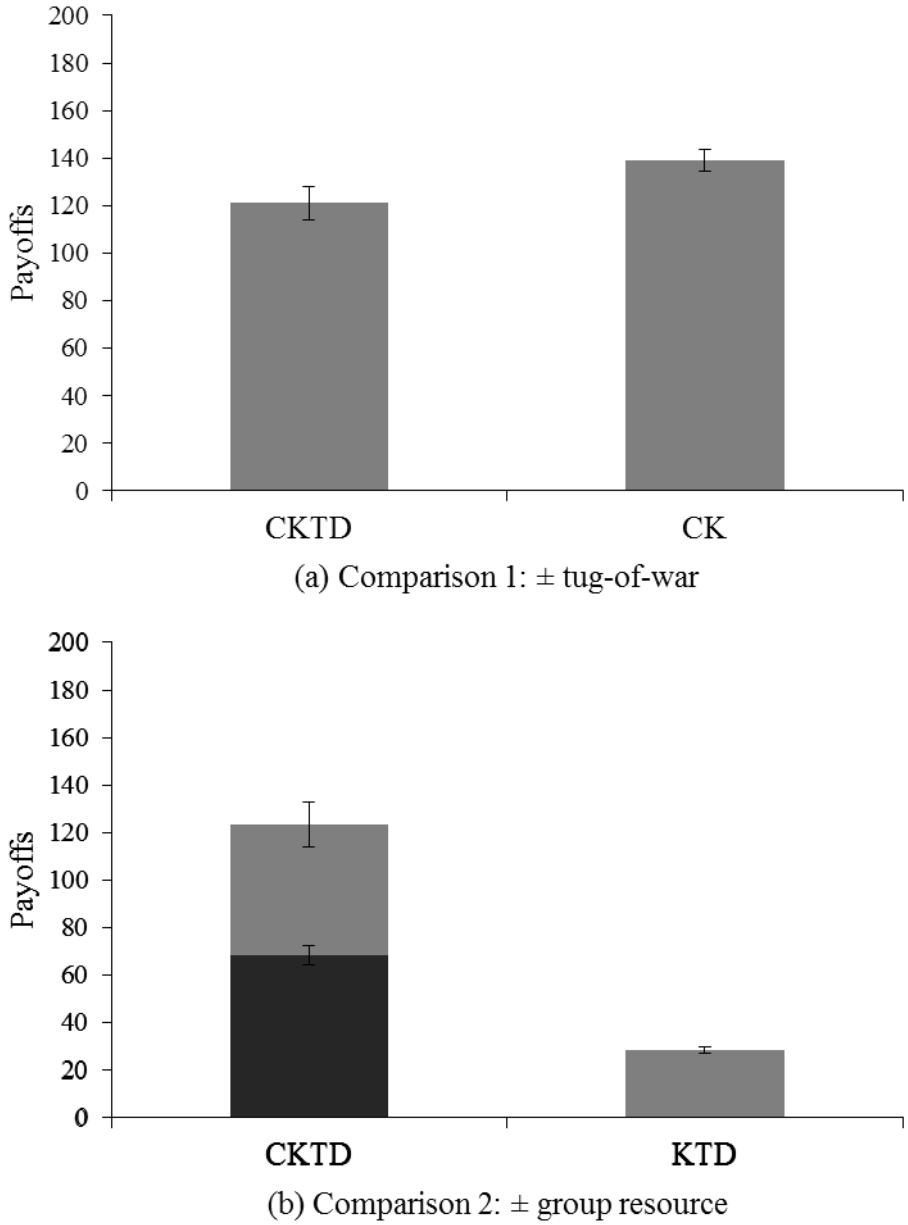

Figure 1.2. Mean (± s.e.) payoffs in lab dollars (L$) per round (means are calculated over 10 rounds of each condition). If all players had contributed all of their money to the group fund each round, the each player's payoff would be L$200; if all players had kept all of their money for themselves each round, each player's payoff would be L$100. (a) Comparison of games with and without the tug-of-war options. (b) Comparison of games with and without the option to contribute to a group fund. Black bar shows players' adjusted payoffs if money contributed to the group fund had not been doubled (i.e. if k=1).

payoffs in the CKTD condition (L$68.5 ± s.e. L$4.2) are still significantly higher than in the KTD condition ($F(1,18)=79.23$, $p<0.001$; Figure 1.2b), suggesting that the difference in payoffs is not simply due to the group resource being doubled. Please note, however, that participants made their decisions in light of the fact that the group resource was doubled, and thus this latter analysis does not explain participants' behavior during the game, but rather provides a reason why their payoffs were higher in the CKTD condition.

In the KTD condition, people kept significantly more money, and invested significantly more in the tug-of-war, than in the CKTD condition (all Fs >24, all ps <0.001, Table 1.1; no effect of order or interaction with order: all Fs <1). This is not surprising, as people had only three investment options in the KTD condition, compared with four in the CKTD condition. Instead, the relevant values are the relative investments: how much people kept for themselves and invested in the tug-of-war, out of the total not contributed to the group fund (i.e. the amount invested in each of keeping, taking and defense, divided by the sum of these three investments). There was no significant difference in people's relative investments between the two conditions (all Fs <2; all ps >0.2). In the KTD condition, people invested more in taking than in defense or amounts kept ($F(1,17)=5.21$, $p=0.017$; Table 1.1), as predicted by the model. Taking money is not a prosocial act: people who take more from their group-mates tend to contribute a lower proportion of their remaining money to the group fund (see appendix).

Table 1.1. Mean (± s.e.) investments in the experimental conditions with and without the option to contribute to a shared group resource (CKTD and KTD respectively). Participants could spread their money among four options in the CKTD condition, compared to three in the KTD condition; in order to control for this, the "relative amount" column shows the amounts participants kept and invested in taking and defense relative to the sum of investments in these three options.

	CKTD condition		KTD condition [c]
	Absolute amount [a]	Relative amount [b]	
Kept for self	13.4 ±2.2	31.3 ±2.1	28.6 ±1.4
Investment in taking	16.9 ±2.0	38.9 ±2.1	41.3 ±2.5
Investment in defense	14.7 ±2.5	29.8 ±2.4	30.1 ±1.6
Contribution	55.1 ±5.5	n/a	n/a
Total [d]	100	100	100

[a] Participants invested significantly lower absolute amounts in taking, defense and keeping in CKTD than in KTD (all Fs >24; all ps <0.001).
[b] There was no significant difference in the relative amounts invested in each of the three options in CKTD versus KTD (all Fs <2; all ps >0.2).
[c] Participants invested significantly more in taking money than in either defense or keeping money ($F(1,17)=5.21$, $p=0.017$) in the KTD condition. In the CKTD condition, the results were in the same direction but were not quite significant (relative amounts: $F(1,17)=3.15$, $p=0.069$; absolute amounts: $F(1,17)=2.60$, $p=0.103$).
[d] Totals may not sum exactly to 100 due to rounding.

DISCUSSION

Contributions to the group resource

People's contributions to a public good were higher when they could also invest in tug-of-war competition (CKTD condition) than when there was no tug-of-war (CK condition); this was true despite having more investment options in the former experimental condition. In addition, the presence of a tug-of-war prevented the decline in contributions over time; such a decline is otherwise typical in public goods games when such competition is absent (CK condition; Dawes and Thaler 1988; Davis and Holt 1993; Ledyard 1995) unless reputations or punishment are present (Wedekind and Milinski 2000; Fehr and Gächter 2002; Barclay 2004). This finding can plausibly be explained by people choosing to contribute more when their own resources were at risk of being taken, since competition over the group resource was not permitted.

Thus, this empirical result supports the game theoretic prediction that in a game with a tug-of-war (CKTD condition), players should contribute to the group resource above a lower threshold return on their investment than in a game without a tug-of-war (CK condition). Two potential criticisms of this result are unlikely to be problematic. Firstly, people may have contributed more in response to being confused by having more options; however, they were tested on their understanding of the game before they were allowed to begin the experiment. Secondly, people contributed in all experimental conditions in the laboratory game even when this was not the optimal strategy predicted by the model for the parameters of our experiment. This is very common in experimental games (Dawes and Thaler 1988; Davis and Holt 1993; Ledyard 1995)

and may occur because people avoid extreme strategies in laboratory games, regardless of whether they are optimal (Kümmerli et al. 2010). Our within-subjects empirical design controls for this by allowing us to analyze the relative differences between experimental conditions.

Tugs-of-war and the tragedy of the commons

Unlike in games with punishment, in this experiment a participant could not target her investments in resource defense and taking towards a specific other player. In addition, people who took more money from others tended to contribute a smaller proportion of their remaining endowment (see analysis in appendix). This suggests that, in contrast to other cases where people spent money in order to reduce the payoffs of the highest earners (Zizzo and Oswald 2001; Zizzo 2004) or lowest contributors (Yamagishi 1986; Fehr and Gächter 2002), investments in taking and defense here were not altruistic sanctions but were simply made in order to maximize one's own personal resources relative to others. This leads to a costly arms race, where people benefit by escalating their competitive investments. Investing in competition reduces the amount of money one can keep or contribute, thus resulting in a tragedy of the commons where everyone is worse off than if no-one had invested in competition (Hardin 1968; Frank 2007; Rankin et al. 2007). The results of the laboratory game reflect this, with people receiving lower payoffs in the CKTD condition than the CK condition.

The lowest payoffs overall were in the KTD condition, where people did not have the option to contribute to a group resource; that is, payoffs in KTD < CKTD < CK. A potential explanation for the higher payoffs in CKTD versus KTD is that all contributions to the group resource were doubled, whereas money in players' personal resources was not. However, had contributions not

been doubled (k=1; "adjusted earnings"), people would still have earned more in the CKTD condition. Players' higher payoffs are thus better explained by the non-contestability of the group resource: equal division precluded people spending money in a competitive arms race. This suggests that the opportunity to contribute to a group resource over which there is no competition may provide a solution to the tragedy of the commons caused by a tug-of-war over personal resources.

Competition and the evolution of shared group resources

In many scenarios outside the laboratory, humans possess resources that can potentially be taken by others, as when the Hadza (Marlowe 2004) and Mikea (Tucker 2004) attempt to hide private shares of food. People also frequently contribute to common resources that are shared among all group members; if these resources are not intrinsically non-excludable, competition over them is nonetheless frequently precluded. For example, there may be no net cost to sharing if the resource is large enough, as in a Lamalera whale hunt (Henrich et al. 2005) or Meriam turtle hunt (Bliege Bird and Bird 1997); alternatively, the cost of not sharing may be high if the resource is divided in public, as among the Nayaka (Bird-David 1990). Such group resources act as "banks" where individuals' investments are protected from scramble competition (i.e. converted into public goods) and possibly even gain value (k>1); indeed, this is likely why monetary banks were initially established (Hildreth 1837; Bolles 1903).

The "tug-of-war arms race over personal resources" hypothesis described here provides one explanation for contribution to non-contestable group resources: that is, the net cost of defending

one's own personal resources and attempting to take others' outweighs the cost of contributing to resources that are shared by all, analogous to models of food-sharing by harassment in non-human primates (Stevens and Stephens 2002; Stevens 2004; Gilby 2006). This hypothesis is not mutually exclusive with other explanations such as reciprocity and risk reduction in uncertain environments (Cashdan 1990). In the present experiment, we isolated the effects of competition by having participants: a) make anonymous decisions, thus reducing reciprocity and reputation; b) receive a fixed amount of money each round, thus not have to buffer uncertainty; and c) never get satiated, and thus not benefit by contributing to others. Please note that this hypothesis provides an ultimate explanation (Tinbergen 1963) for contribution to shared group resources, and does not attempt to elucidate individuals' proximate motivations.

In sum, the implications of this study are threefold. Firstly, the theoretical and empirical results suggest that the opportunity to contribute to an equally shared group resource (especially one that has the potential to earn interest) helps to limit mutually destructive competition over personal resources. Secondly, this finding is not specific to humans, but applies to any social groups in which individuals can compete over personal resources (Reeve et al. 1998) and contribute to shared group resources. For example, costly competition among hymenopteran workers over male production (Hammond and Keller 2004; Wenseleers et al. 2004) may select for contribution to the queen's reproductive success as a non-excludable shared resource. By drawing on approaches developed in different disciplines, such as tug-of-war theory and economic games, we can uncover universal evolutionary principles governing the balance between cooperation and conflict across the animal kingdom. Finally, much environmental and social conflict in human societies arises over the contribution to and division of personal and shared resources

(Ostrom et al. 1999; Dietz et al. 2003) and elucidating the evolutionary explanations for these behaviors can help us more effectively manage them (Ostrom et al. 1992; Penn 2003; Janssen et al. 2010; Rustagi et al. 2010).

APPENDIX

1. Model

a. Finding endpoint maxima

We found no intermediate solution to $dw_y/dy = 0$, which means there is no value of y between 0 and v that maximizes a player's payoff (i.e. $0<y^*<v$). Thus, a player's optimal strategy is to contribute either all ($y^*=v$) or none ($y^*=0$) of her resources; that is, y^* is an endpoint maximum. We determine which of these boundary solutions ($y^*=0$ or v) maximizes a player's payoff by examining dw_y/dy: if $dw_y/dy<0$, then the lower boundary gives the fitness maximum; if $dw_y/dy>0$, the upper boundary does. We find that $dw_y/dy = 0$ when $\frac{k}{n}=1$, such that when $k>n$, players should contribute everything ($y^*=v$), and when $k<n$, they should contribute nothing ($y^*=0$).

We apply the same procedure to w_{xyz} (i.e. the payoff in game with a tug-of-war) to determine which boundary value maximizes a player's payoff.

b. Effectiveness of defending relative to taking resources

The effectiveness of a given investment in resource defense (x^*) relative to an investment in taking from others (z^*) is given by the factor b. We simultaneously solve $\delta w_{xyz}/\delta x=0$ and $\delta w_{xyz}/\delta z=0$ for the fitness-maximizing values x^* and z^* (see main text), and find that:

Equation S1.1

$$x^* = \frac{(b(n-1)-n+2)(n-1)v}{b^2(n-1)^2 + b(n^2-1) - n(n-2)}$$

$$z^* = \frac{b(n-1)^2 v}{b^2(n-1)^2 + b(n^2-1) - n(n-2)}$$

When b=1, these values simplify to the values for x^* and z^* given in the main text (Equation 1.5). In addition, note that the numerator of x^* is only >0 when $b>\frac{n-2}{n-1}$. Therefore, if $b\leq\frac{n-2}{n-1}$, the optimal strategy is to invest $x^*=0$ in defense, because defending one's resources is ineffective. If b is above this critical value, the optimal investment in defending (x^*) relative to taking (z^*) is:

Equation S1.2

$$\frac{x^*}{z^*} = \frac{b(n-1)-n+2}{b(n-1)}$$

When b=1, this simplifies to $\frac{1}{n-1}$: that is, a player should invest n-1 times more in taking from others than in defending. This is because any investment in taking (x^*) is spread among the n-1 other group members (see main text).

In order to determine how the relative investments in defending and taking vary with *b*, we evaluate the derivative of Equation S1.2 with respect to *b*:

Equation S1.3

$$\frac{d\frac{x^*}{z^*}}{db} = \frac{n-2}{b^2(n-1)}$$

Given that $n>2$, this derivative is always positive, and thus as *b* increases (that is, resource defense increases in effectiveness relative to stealing), a player should increase her investment in defense relative to stealing.

2. Comparison of CKTD versus CK experimental conditions

a. Controlling for the number of investment options

In order to control for the extra options in the game with a tug-of-war (CKTD), we can analyze people's contributions relative to the amount they kept for themselves (i.e., amount contributed / [amount contributed + amount kept]), as these were the only options they had in both experimental conditions. In this analysis of relative contributions, people's relative contributions in the CKTD condition (L$76.1 ± s.e. L$4.0) were even higher than the contributions in the CK condition (L$39.0 ± s.e. L$4.6; $F(1,24)=55.07$, $p<0.001$).

b. Keeping money

In the standard public goods game (CK condition), the amounts people keep for themselves are simply whatever they do not contribute to the group. Therefore, if people contribute more when there is a tug-of-war (CKTD condition; see main text), this necessarily implies that people keep less for themselves in the CKTD condition ($14.3 ± s.e. L$2.0) than in the CK condition (L$61.0 ± s.e. L$4.6; $F(1,24)=118.05$, $p<0.001$).

Similarly, if we control for the number of investment options in the CKTD condition by analyzing the amount kept relative to the amount contributed (i.e., amount contributed / [amount contributed + amount kept]; see section 2a above), the relative amount people keep is significantly lower in the CKTD condition (L$23.9 ± s.e. L$4.0; $F(1,24)=55.07$, $p<0.001$).

c. Effects of order on contributions in comparison 1

The order of experimental conditions (CKTD first versus CK first) had a significant effect on people's contributions over time (Order x Round interaction: $F(9,216)=4.39$, $p<.001$, other effects or interactions involving order are all $F<1$), so we present each order separately below.

When participants played CKTD first, contributions were significantly higher in the CKTD condition (L$54.0 ± s.e. L$5.8) than in the CK condition (L$35.9 ± s.e. L$6.6; $F(1,12)=7.66$, $p=0.017$). There was a significant interaction between experimental condition and round number

($F(9,108)=3.72$, $p<0.001$): in the CK condition, contributions fell over time ($F(9,108)=6.69$, $p<0.001$), whereas contributions did not change in the CKTD condition ($F<1$, n.s.).

When participants played CK first, contributions were marginally significantly higher in the CKTD condition (L$52.8 ± s.e. L$6.5) than in the CK condition (L$42.1 ± s.e. L$6.6; $F(1,12)=3.40$, $p=0.090$). There was a significant interaction between experimental condition and round number ($F(9,108)=7.53$, $p<0.001$): in the CK condition, contributions fell over time ($F(9,108)=3.81$, $p<0.001$), whereas contributions increased in the CKTD condition ($F(9,108)=5.10$, $p<0.001$).

Thus, despite this interaction, the major results (higher contributions in the CKTD condition, contributions falling over time in the CK condition but not the CKTD condition) are independently replicated in the two different orders. Order was counterbalanced across sessions, with 13 groups playing CKTD first and 13 playing CK first.

3. Taking money and moralistic punishment

One possible explanation for taking money is that it is a form of moralistic punishment towards low contributors. This is unlikely to be true for two reasons. Firstly, participants in our experiment could not target their taking towards specific people. Secondly, people who took more money from others tended to be non-contributors themselves. We tested the latter by calculating a "contribution ratio" for each participant based on how much they contributed in the CKTD condition relative to how much they kept, i.e. [C/(C+K)]. This automatically controls for

the fact that people who take more will naturally have less remaining to contribute. We carried out a repeated-measures general linear model to see whether these contribution ratios differed between the person in each group who took the most from others, took the second-most from others, the third-most, and the least.

If taking is a form of moralistic punishment, then people who take more should have higher contribution ratios, because such moralistic punishment is usually carried out by cooperators (Fehr and Gächter 2002; Barclay 2006). We did not find this in our experiment; indeed, the opposite was true: players who took the most, second-most, third-most, and least in each group had average contribution ratios of 0.64 (± s.e. 0.05), 0.68 (± s.e. 0.04), 0.76 (± s.e. 0.04), and 0.80 (± s.e. 0.04), respectively; the omnibus F-test was significant ($F(3,126)=6.62$, $p<0.001$), as was the linear contrast ($F(1,42)=15.16$, $p<0.001$). Thus, those who took more than their group-mates also contributed less than their group-mates. Results are very similar if we rank players based on how much they spent on taking plus defending (instead of just taking). The order of conditions had no effect or significant interactions in either case (all Fs<1).

The results are a little more complicated if we analyze the two experimental contrasts separately (CKTD versus CK, and CKTD versus KTD), given that this factor does interact with how much a person takes relative to other group members ($F(3,126)=7.16$, $p<0.001$). The following results are unlikely to be theoretically interesting, but we present them here for completion. When participants played the CKTD and KTD conditions, taking was negatively related to the contribution ratio, as it was in the above analysis: players who took the most, second-most, third-most, and least in each group had average contribution ratios of 0.51 (± s.e. 0.07), 0.72 (± s.e.

0.06), 0.74 (± s.e. 0.06), and 0.83 (± s.e. 0.04), respectively; the omnibus F-test was significant ($F(3,54)=12.79$, $p<0.001$), as was the linear contrast ($F(1,18)=32.34$, $p<0.001$). The situation was different when participants played the CKTD and CK conditions: there were different contribution ratios between players who took the most (0.78 ± s.e. 0.06), second-most (0.64 ± s.e. 0.06), third-most (0.79 ± s.e. 0.05), and least within each group (0.78 ± s.e. 0.05), ($F(3,72)=2.75$, $p=0.049$), but these differences were due to quadratic and cubic trends (Fs(1,24)=4.39 and 4.85, ps = 0.047 and 0.038, respectively) instead of a linear increase. Although this scenario is more complicated, both cases show that people who take more do not contribute more, so it is unlikely that taking from others is a form of moralistic punishment.

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CHAPTER 2

WITHIN-GROUP COMPETITION REDUCES COOPERATION AND PAYOFFS IN HUMAN GROUPS

Jessica L. Barker, Pat Barclay and H. Kern Reeve

Social organisms in many taxa cooperate to produce resources that are shared among group members. Some cooperatively produced resources may be monopolized by individuals who invest in within-group competition, but these have largely been overlooked in empirical and theoretical research on human cooperation, which has focused on non-contestable public goods. In this study, we allow for the potential of within-group competition over cooperatively produced resources, and use a game theoretic "tug-of-war" model and empirical test to show that such competition decreases the degree of cooperation within human groups, and hence decreases group members' payoffs. Our study thus sheds light on how cooperative production and equal division of shared resources may have evolved, expands on current models of human cooperation to reflect the many natural conditions with opportunities for within-group competition, and demonstrates unifying principles in cooperation and competition across the animal kingdom.

Barker JL, Barclay P, Reeve HK. 2012. Within-group competition reduces cooperation and payoffs in human groups. Behavioral Ecology 23:735-741.

INTRODUCTION

Social organisms from many taxa, from bacteria (Rainey and Rainey 2003) to mammals (Packer and Ruttan 1988), often share cooperatively produced resources. Some such resources are intrinsically non-excludable (public goods, as strictly defined), while others are potentially monopolizable by certain group members, who may then gain direct fitness benefits from obtaining larger shares relative to other individuals in the group (Williams et al. 2002). Studies of cooperation in humans have focused on non-excludable public goods such as clean air or tax-funded infrastructure, which has led to the implicit assumption that all important group resources are automatically divided equally, even when there is the potential for monopolization (Dawes 1980; Hawkes 1993; Fehr and Gächter 2000; Smith and Bliege Bird 2000; Milinski et al. 2002; Barclay 2004). In this study, we relax the assumption of automatic equal resource division in human groups by applying the principles of "tug-of-war" models used to analyze conflict in non-human animals (Reeve et al. 1998; Reeve and Hölldobler 2007; Shen and Reeve 2010). Studies of within-group competition on humans have examined competition in other contexts, such as access to relationships (Fehr and Schmidt 1999; Barclay and Willer 2007), but here we provide an explicit test of how within-group competition over shared resources affects people's payoffs and levels of cooperation.

Competition over cooperatively produced resources

In this study, we concentrate on cooperatively produced, shared resources that are (a) depletable, i.e. if one individual takes more then there is less available for others; (b) contestable, i.e. the size

of each individual's share is not fixed; and (c) subject to a trade-off, due to limited time and energy budgets, between cooperative resource production and selfish investment in competition to increase the size of one's own share. Such resources are well documented in non-human animal societies: for example, an individual's share of cooperatively hunted food may be determined by contest competition (coatis *Nasua narica*: Gompper 1996; chimpanzees *Pan troglodytes*: Watts and Mitani 2002, Williams et al. 2002) or dominance rank (salmonid fish *Oncorhyncus masou macrostomus*: Hakoyama and Iguchi 1997; chimpanzees: Fruth and Hohmann 2002, Williams et al. 2002). However, investing in cooperation to obtain this food for the group may be individually costly (Fruth and Hohmann 2002), reducing an individual's chance of increasing its rank and reproducing in the future, e.g. in social wasps (*Polistes dominulus*: Cant and Field 2001; *Liostenogaster flavolineata*: Field et al. 2006). Likewise, reproductive opportunities may be cooperatively produced (Watts 1998), if individuals can only access mates by joining coalitions. This precludes coalition members from investing in other activities (Smith et al. 2010), such as competing for a share of the mating opportunities, which are often distributed unequally among coalition members, for example in dunnocks *Prunella modularis* (Davies 1992), dolphins *Tursiops aduncus* (Connor et al. 2001), baboons *Papio cynocephalus cynocephalus* (Noë 1990), dwarf mongooses *Helogale parvula* (Rood 1990), and cheetahs *Acinonyx jubatus* (Caro and Collins 1987).

Although the balance between cooperation and conflict, and how this balance affects the degree of equal sharing, has been a major research focus in the field of behavioral ecology (Vehrencamp 1983; Keller and Reeve 1994; Sherman et al. 1995), within-group competition over cooperative group production has largely been overlooked in studies of human cooperation. In the classic

"public goods" economic games typically used to investigate human cooperation in the laboratory, equitable division of resource production is usually forced on the players, so there is no opportunity for within-group competition (e.g. Davis and Holt 1993; Ledyard 1995; Fehr and Gächter 2000; Puurtinen and Mappes 2009; Kümmerli et al. 2010). Many potentially contestable resources are indeed divided relatively equitably within human groups, for example food in hunter-gatherer societies (Kaplan and Hill 1985; Smith and Bliege Bird 2000; Hawkes et al. 2001). However, in these cases, equal sharing is not automatic, and often results from costly enforcement of social institutions (Boehm 1993; Bowles et al. 2003; Gurven 2004) or because there are diminishing returns from investment in defending a share that is too large for oneself (Blurton Jones 1984). In other cases, there is competition over depletable and non-monopolizable resources: male competition over females occurs in hunter-gatherer societies (Knauft 1991), and in industrialized nations, there is high competition over possession of resources to produce fuel and food (Hardin 1968, 1998; Penn 2003). Many types of social competition have been described as "arms races" (Axelrod 1984; Frank 2007), a term which connotes costly investment by multiple parties in escalated competition that reduces individuals' ability to invest in cooperation (or indeed anything else) and that is detrimental to all. There is therefore a need to test explicitly the effect of within-group competition on cooperation.

Modeling within-group competition over group resources

Within-group competition and variation in resource division can be quantified using game theoretic analysis: for example, "tug-of-war" models predict evolutionarily stable energy investments in costly competition (Reeve et al. 1998; Reeve and Hölldobler 2007; Shen and

Reeve 2010). In a simple tug-of-war, resources are divided according to the relative investments individuals make in competition and the asymmetry in their competitive efficiency. For example, if individual A invests twice as much as individual B in competition over shared resources, and if the two individuals have an equal competitive efficiency, then A obtains twice as large a fraction of the resources. Tug-of-war models successfully predict both the degree of equitable division of resources according to the values of the efficiency parameters and relative competitive investments, and how much resource is used up in competition. These models have been applied to both small and large societies of invertebrates and vertebrates, such as allodapine bees *Exoneura nigrescens* (Langer et al. 2004), meerkats *Suricata suricatta* (Clutton-Brock et al. 2001), lions *Panthera leo* (Packer et al. 2001) and wood mice *Apodemus sylvaticus* (Gerlach and Bartmann 2002), but tug-of-war theory has not yet been applied explicitly to humans. However, because depletable and contestable resources are shared among humans living in groups, and because human and non-human coalitionary behaviors are similar (Harcourt and de Waal 1992), we expect humans to engage in within-group tug-of-war competition over shared resources, as do other animals.

We hypothesize that when faced with choosing how much of one's own personal resources to (a) keep for oneself, (b) cooperatively contribute towards producing group goods, or (c) selfishly invest in competing for a larger share of the group goods, people may increase their payoffs by investing more in competition relative to the other two options. Given that there is a tradeoff between cooperatively contributing to the shared resource and competing for it, we predict that when people have the option to engage in within-group competition, (1) people will invest less in cooperatively producing the shared resource, and (2) the size of the shared resource will be

smaller. We tested these predictions both mathematically, in a game theoretic model, and empirically, in a laboratory economic game.

MODEL

We first develop a simple model that inserts a tug-of-war into a basic public goods game. Each of *n* group members begins with an amount of personal resource *t*. Of this resource, individuals keep an optimal amount *s**, invest an optimal amount *z** in competition, and contribute *t*-*s**-*z** to the group. Contributions are summed and multiplied by *k*, so there is a collective benefit to contributing. This "group productivity" is then divided among all group members according to their relative investments in competition (the "tug-of-war"): if any given focal individual invests *z* in competition, and the *n*-1 other group members invest *z**, then the fraction *f* of group productivity that the focal individual obtains is:

Equation 2.1

$$f = \frac{z}{z + (n-1)z^*}$$

It is stipulated that if all investments in competition are zero (*z* and *z** = 0), the resource is shared equally, as is typically assumed in most human cooperation experiments.

This focal individual keeps a fraction *s* of its personal resource *t*. Its total payoff (i.e. the sum of resources kept for itself plus the share of group productivity obtained through the tug-of-war) is therefore:

Equation 2.2

$$s + fk[(t - s - z) + (n - 1)(t - s^* - z^*)]$$

To find the strategies *s* and *z* that maximize an individual's payoff, we partially differentiate Equation 2.2 with respect to *s* and to *z*, and set each partial derivative equal to zero. We use the second derivative test to verify that these are fitness maxima. The evolutionarily stable solutions (Nash equilibria) occur when the fitness maximizing values of *s* and *z* are the same as *s** and *z**. The evolutionarily stable solutions to this tug-of-war game depend on the group's productivity relative to its size. If $k > n$, a group member should invest

Equation 2.3

$$z^* = \frac{t(n-1)}{n}$$

in competition and contribute all of the rest to the group's shared resources. However, if $k < n$, the individual should keep all of its resources for itself ($s^* = t$; no competition and no contribution).

We then substitute these fitness-maximizing values for s^* and z^* into Equation 2.2 to find an individual's payoff at equilibrium. If $k > n$, a group member obtains a payoff of value kt / n, and if $k < n$, a group member obtains t.

We can now compare this tug-of-war game with a game where individuals cannot invest in competition (z and $z^* = 0$), i.e. where group resources are automatically divided equally (a classic public goods game). In the automatic equal division game, the optimal solutions are (a) if $k > n$, contribute everything ($s^* = 0$), and obtain a payoff of value kt; (b) if $k < n$, keep everything ($s^* = t$), and therefore obtain a payoff t.

Thus, the effect of including a possible tug-of-war in a classic public goods game, i.e. of players having the option to compete over shares of group productivity, is that individuals will (1) be less cooperative and (2) obtain lower payoffs than when the resource is automatically equally divided. This yields a kind of "tragedy of the commons" (Hardin 1968) where the evolutionarily stable strategies leave all players worse off (i.e. cannot be invaded by more cooperative strategies). Since there is a possibility of a tug-of-war whenever resources are contestable, the actual levels of cooperation in nature in such cases are expected to be significantly lower than as described by public goods models with automatic resource division.

Importantly, note that although it is never strictly rational to cooperate in our experiment because the multiplier k is less than the group size n (k=2 and n=4), we nevertheless predict some non-zero level of cooperation in both conditions. This is because many empirical studies demonstrate that people regularly contribute to group productivity even when $k < n$ and in experimental

conditions where there is no incentive to cooperate (Davis and Holt 1993; Ledyard 1995; Fehr and Gächter 2000; Fischbacher et al. 2001; Barclay 2004). As such, the relevant predictions for our experiment are the relative differences between the tug-of-war and equal division games, not the absolute contributions or payoffs (Kümmerli et al. 2010).

METHODS

Empirical test

We recruited 48 voluntary participants from the Cornell University community (27 females and 21 males; mean (±s.e.) age: 20.73 ±1.64 years) to play an economic game, programmed using z-Tree software (Fischbacher 2007). Participants played the game in groups of four, and sat at computer terminals visually isolated from other group members; they did not know how many rounds of the game they would play. All decisions were confidential and only associated with code numbers; all methods were approved by the Institutional Review Board for Human Participants. Players read an instruction program and completed a quiz to test their understanding of the game before they could begin the experiment itself. Participants earned "lab dollars" (L$), which were exchangeable to US dollars at a rate of 300:1, plus a baseline payment of US$2. Mean (±s.e.) earnings were 9.70 ±1.11 US dollars, depending upon participants' decisions during the game. Each game consisted of two experimental conditions.

Equal division condition

Each round, each player received L$100, and decided how much to invest in a "personal fund" versus cooperatively contribute to a "group fund" (standard public goods game, e.g. Davis and Holt 1993; Ledyard 1995; Fehr and Gächter 2000; Fischbacher et al. 2001; Barclay 2004). Contributions to the group fund were doubled and redistributed equally among all participants. Therefore, each player's payoff at the end of each round was equal to her investment in the personal fund plus one quarter of the doubled group fund. Each player saw a screen at the end of each round displaying her payoff and the overall contribution to the "group fund" that round.

Tug-of-war condition

In addition to the options in the equal division game, players could invest any of their L$100 in competition over shares of the group fund (termed "extraction" to avoid framing problems). In this experimental condition, each individual's share of the doubled group fund was determined by her relative investment in competition: e.g. if players A, B, C and D invested L$10, L$20, L$30, and L$40 respectively in competition, then player A got 10/(10+20+30+40) = 1/10 of the group fund. If a player invested nothing in competition when others did do so, she did not benefit from the group fund; if no players invested in competition, the group fund was split equally. In sum, each player's payoff each round was equal to her investment in her personal fund plus her share of the doubled group fund, with shares being determined by relative investments in competition (Equation 2.1). At the end of each round, each player saw a screen displaying her

payoff, the overall contribution to the "group fund", and the fraction of the group fund she obtained that round.

Statistical analyses

We used a within-subjects design: participants played 10 rounds of each condition, with order of conditions counterbalanced between groups. To control for interdependence within groups, we treated each group of 4 as an N of 1. We analyzed group contributions using a general linear model (SPSS 17.0) with experimental condition (tug-of-war versus equal division) and round (10 rounds per condition) as within-subjects variables, and with the order of conditions as a between-subjects variable.

RESULTS

Cooperative contributions to group productivity

Contributions were lower in the tug-of-war than in the equal division condition ($F_{1,10} = 20.83$, $p = 0.001$), supporting our prediction. The difference in contributions between the tug-of-war and equal division conditions was so robust that it was independently significant in both orders of experimental condition (equal division first: $F_{1,5} = 15.4$, $p = 0.011$; tug-of-war first: $F_{1,5} = 7.26$, $p = 0.043$; Figure 2.1), and order did not interact with other variables (all Fs < 1.1), such that the two orders could even be considered independent replications of each other.

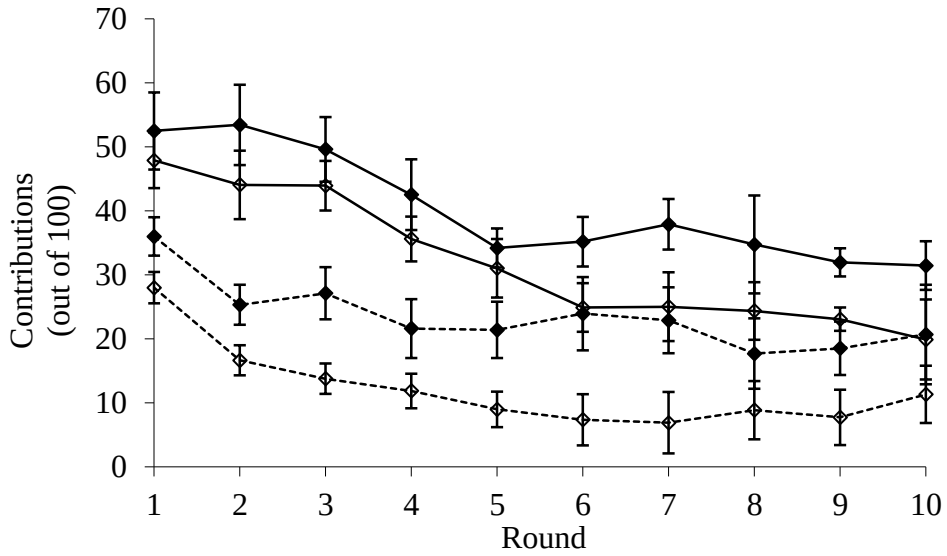

Figure 2.1. Mean contributions to the group fund out of 100 (± s.e.) when the group fund was divided equally (equal division: solid lines) versus divided according to investment in within-group competition (tug-of-war: dotted lines). Open circles represent groups where the equal division condition came first, and closed triangles represent groups where the tug-of-war condition came first. Within-subjects error bars were calculated by factoring out individual differences in contributions (Cousineau 2005).

Consistent with past research in public goods games (e.g. Davis and Holt 1993; Ledyard 1995; Fehr and Gächter 2000; Fischbacher et al. 2001; Barclay 2004), contributions fell over time ($F_{9,90}$ = 12.88, $p < 0.001$) in both experimental conditions (equal division: $F_{9,90} = 10.73$, $p < 0.001$; tug-of-war: $F_{9,90} = 5.38$, $p < 0.001$). There was a significant round by condition interaction ($F_{9,90} = 2.63$, $p = 0.010$): contributions fell more under equal division than under tug-of-war, most likely because they had further to fall from.

Controlling for investments in competition

One might argue that contributions were lower in the tug-of-war simply because participants had an extra option for investment (i.e., competition), in addition to contribution. To control for participants' having less money available to contribute in the tug-of-war, we analyzed contributions as a percentage of the money remaining after investment in competition: we divided all contributions by the quantity "100 minus competition". Under this new analysis, contributions (as a proportion of the amount available) were still lower under tug-of-war than under equal division ($F_{1,10} = 5.92$, $p = 0.035$; Figure 2.2). This further supports our argument that competition decreases cooperation within social groups. Contributions decreased across rounds in this new analysis also ($F_{9,90} = 9.90$, $p < 0.001$), but the round by condition interaction was no longer significant ($F < 1$).

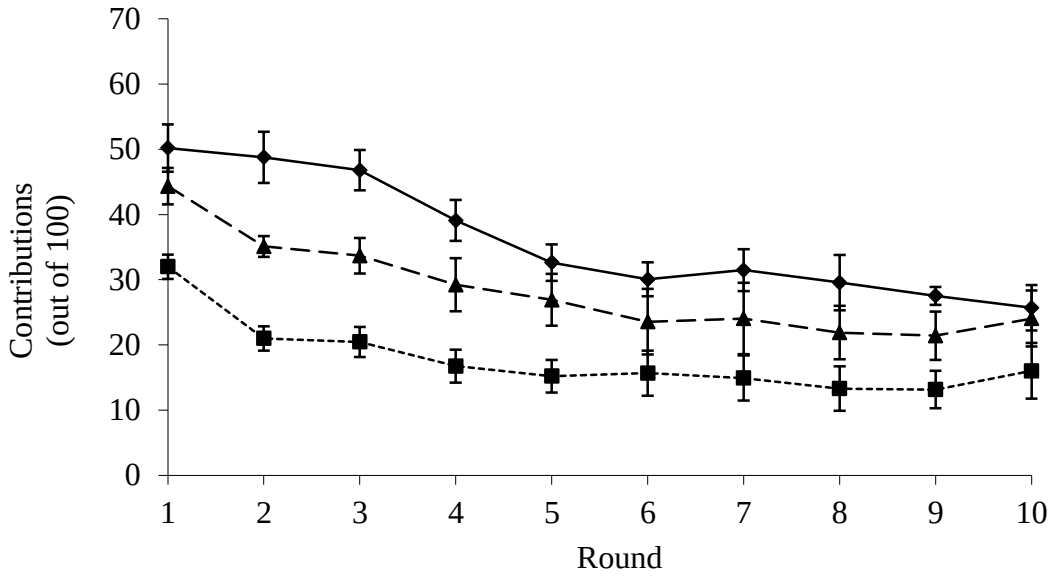

Figure 2.2. Mean contributions to the group fund out of 100 (± s.e.) when the group fund was divided equally (equal division: solid line) versus divided according to investment in within-group competition (tug-of-war: dotted line). The dashed line represents contributions in the tug-of-war as a percentage of the amount remaining after investing in within-group competition. All three lines display data both from groups where the equal division condition came first and from those where the tug-of-war came first. Within-subjects error bars were calculated by factoring out individual differences in contributions (Cousineau 2005).

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Amount kept

An alternative hypothesis for the decreased contribution in the tug-of-war condition is that participants were confused by more options being available: for example, participants may have experimented with both options (keeping and competition) and responded by keeping money instead of contributing it. If this is true, we should see participants keeping more money for themselves in the tug-of-war condition than under equal division. Instead, the opposite was true: participants actually kept more money for themselves in the equal division condition than under tug-of-war (means (±s.e.) for equal division: 63.8 ±6.5; for tug-of-war: 55.9 ±6.9, $F_{1,11} = 6.54$, $p = 0.027$), which falsifies this hypothesis. In addition to testing participants' understanding before they started the experiment, we asked participants in an anonymous post-experiment questionnaire whether the instructions had been clear and what strategies they adopted during the game; 91% of players indicated that they completely understood the instructions. Thus, the lower contributions in the tug-of-war condition are better explained as being a result of the competition rather than being due to confusion.

Payoffs

Players' payoffs (i.e., total earnings in the game from investment in the personal fund plus shares of the group fund) were higher in the equal division condition than in the tug-of-war (mean earnings (±s.e.) in L$: equal division: 1362.79 ±65.29; tug-of-war: 916.54 ±16.00; paired $t_{11} = 6.71$, $p < 0.001$; Figure 2.3), as predicted. If all participants had contributed everything in every round of a given condition, each participant would have earned L$2000 (US$6.67, excluding

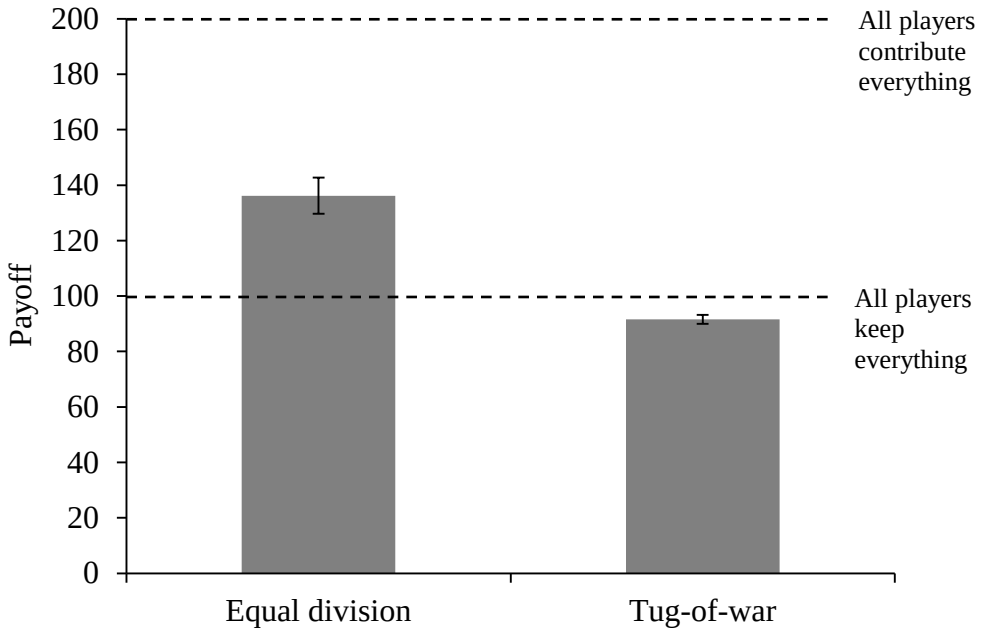

Figure 2.3. Mean payoffs (± s.e.) in lab dollars at the end of each experimental treatment (i.e. after 10 rounds). Within-subjects error bars were calculated by factoring out individual differences in contributions (Cousineau 2005).

US$2 baseline payment); if all players kept all their money, each player would have earned $1000 (US$3.33, excluding US$2 baseline payment). In the tug-of-war, people expended resources in competition, rather than contributing towards production of the shared group resource, and thus players did worse overall than if they had simply kept all their money (one-sample $t_{11} = 5.28$, $p < 0.001$).

DISCUSSION

The tug-of-war model predicted that the option to invest in competition over group productivity leads to people (a) contributing less and (b) obtaining lower payoffs. The results of the experimental game support both of these predictions. The decrease in cooperation in the tug-of-war condition could not be explained by participants simply withholding more money or having less available to contribute, but instead arose from participants contributing a smaller relative amount to group productivity. These experimental results reflect many situations outside the laboratory where competition over real-life resources may reduce cooperative production and hence individuals' payoffs. For example, parties in dispute over land may spend money in a military arms race, instead of spending money on using the land to produce resources that can then be shared; rivals for the leadership of a political party may harm their party's chances of electoral success by engaging in fierce within-party competition; and if academic collaborators put time and energy into contesting first authorship, they may produce a lower quality collaborative project than if they devoted all of their resources to the project itself. In some non-human primates, the mere potential for resource monopolizability, regardless of whether it is

realized, can reduce cooperation in laboratory tasks (brown capuchins *Cebus apella*: de Waal and Davis 2003; chimpanzees: Melis et al. 2006).

Given the parameters in our experiment, notably with $k<n$, the model predicted that the optimal decision is to keep all of one's own resources, regardless of the potential for competition. However, people still contributed in both experimental conditions in our laboratory game, despite not having any incentive for cooperation, such as between-group competition (Bornstein and Ben-Yossef 1994; Puurtinen and Mappes 2009) or reputation (Yamagishi 1986; Nowak and Sigmund 1998). Classic "public goods games," which by default have equal division, have yielded the same results in this regard (e.g. Davis and Holt 1993; Ledyard 1995; Fehr and Gächter 2000; Fischbacher et al. 2001; Barclay 2004). Players' suboptimal decisions may simply be because people avoid extreme options in laboratory games, regardless of whether they are optimal (Kümmerli et al. 2010) or due to unconscious concerns about reputation (Haley and Fessler 2005; Burnham and Hare 2007). In order to control for this, each participant in our experiment played both experimental conditions: the relevant results are therefore contributions in one condition relative to the other, and the absolute values are not important.

Effects of competition on cooperation and productivity

In a tug-of-war model, the amount of group resources that each individual obtains is a product of (a) the total pool of resources produced by the group, and (b) the fraction of this total that each individual obtains relative to other group members; these are determined by within-group cooperation and between-group competition (West et al. 2006; Reeve and Hölldobler 2007) and

within-group competition (Reeve et al. 1998; Reeve and Hölldobler 2007; Shen and Reeve 2010) respectively. An individual can maximize its payoff by free-riding on others' contributions to group productivity, and, if there is the potential for competition, by investing more in competition relative to other group members at the expense of contributing. This is likely to result in an arms race of escalating competitive investments (Axelrod 1984; Frank 2007), the intensity of which may vary depending on the abundance and monopolizability of group resources, such as cooperatively hunted meat (Blurton Jones 1984; Bliege Bird and Bird 1997). Due to the trade-off between competition and cooperation, this reduces group productivity and thus may lead to a "tragedy of the commons" (Hardin 1968; Rankin et al. 2007), leaving all group members worse off than if none had invested in competition. Individuals in these competitive groups will have lower fitness than individuals in groups with higher cooperation (Reeve and Hölldobler 2007; Wilson and Wilson 2007), such that each individual would individually benefit from suppression of competition (West et al. 2006).

Given the significant reduction in people's payoffs in the tug-of-war condition in our experiment, we predict selection for mechanisms to reduce within-group competitive conflict and increase the relative benefit of within-group cooperation (Ratnieks and Reeve 1992; Bowles et al. 2003; Bowles 2006; West et al. 2006). This prediction may explain the fact that many contestable and depletable resources outside the laboratory are, in practice, usually shared equally, for example big game in hunter-gatherer societies (Knauft 1991; Hawkes 1993; Smith and Bliege Bird 2000). However, this egalitarianism is not necessarily cost-free and automatic, but may be enforced (Boehm 1999). Allowing for within-group competition may thus provide insight into why there was selection for equitable division of potentially contestable resources. We suggest that (1)

equitable division was preceded by high within-group competition, since individuals benefit by escalating their competitive investments relative to other group members, and (2) the detrimental effect of this competition allowed selection for "individually costly, group beneficial" (Bowles et al. 2003) suppression mechanisms, via genetic selection or via cultural evolution and the differential survival of cultural norms (Boyd and Richerson 2009).

These mechanisms may include policing (Frank 1995; Frank 2003; El Mouden et al. 2010) or social institutions such as monogamy and food sharing norms (Bowles et al. 2003) and self-government (Ostrom et al. 1992), but will likely differ in different societies and for different resources. Across cultures, one might predict (1) less investment in and reliance on cooperatively-produced resources if those shared resources are contestable, or need to be competed over because they are in short supply; (2) higher cooperation in experimental economic games in cultural groups habitually exposed to contestable shared resources than in groups exposed to non-contestable resources; and (3) greater investment and reliance on cooperative resources in species or cultural groups that have mechanisms for equal sharing. Future research should investigate the variation in resource competition and suppression mechanisms both among and within cultures. In addition, since payoffs may be more inequitable when there is more within-group competition, our results suggest that there may be selection for reproductive leveling mechanisms to reduce fitness differences among group members, an idea which has not been explicitly tested in humans (Bowles 2006).

Summary

This study demonstrated mathematically and empirically the detrimental effect of within-group competition on individuals' cooperation, and therefore their payoffs. The novel result that a within-group tug-of-war can lead to a tragedy of the commons may explain why many human groups have evolved mechanisms to ensure contestable resources are shared equally (Knauft 1991; Boehm 1999; Bowles 2006). Allowing for the potential of within-group competition in laboratory games lets us model a broader range of natural situations more accurately, an important goal in the study of human cooperation (Janssen et al. 2010). Additionally, acknowledging competition within human groups helps us draw parallels with the dynamics of cooperation and conflict in non-human social animals (Harcourt and de Waal 1992), and suggests that the trade-off between competition and cooperation is likely a universal principle across the animal kingdom (de Waal and Davis 2003). Finally, given that human competition (and hence lack of cooperation) over depletable resources such as oil, cod stocks, and clean water from irrigation systems (Hardin 1968; Hardin 1998; Ostrom et al. 1999; Dietz et al. 2003; Penn 2003) has led to many current environmental problems, we suggest that recognizing the need to reduce this competition will allow more effective management of these issues.

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CHAPTER 3

INTERGROUP COMPETITION AND THE TRADEOFF BETWEEN COOPERATION AND CONFLICT: TESTING THEORETICAL PREDICTIONS IN PAPER WASPS

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Intergroup competition is theoretically predicted to favor increased cooperation within social groups. There is much empirical support for this in human and non-human vertebrate societies, but although intergroup competition has been proposed as an explanation for "superorganism"-like insect colonies, it has not explicitly been tested in eusocial insects. In addition, a common assumption in studies of cooperation and conflict in social groups is that all effort not expended in within-group competition is invested in cooperation; this is not the case in many societies, where individuals may benefit by conserving resources for future reproduction. In this study, we relax this assumption of a direct tradeoff, and generate alternative game theoretic predictions of the effect of intergroup competition on within-group competition and cooperation. We tested these predictions experimentally in the primitively eusocial paper wasp *Polistes dominulus*. In a field experiment, we found that workers' nest departure rate, aggression rate and nest activity increased when we transplanted nests closer together. In the lab, nests paired with a competing nest did not increase or decrease their aggression, foraging or activity levels, but the relationships between these behaviors were different. In the absence of a competing nest, a change in aggression within a nest over time was positively correlated with a change in foraging rate, and negatively correlated with a change in activity. However, in the presence of a competing nest, a change in aggression is positively correlated with a change in activity. These results do not give

full support for the predictions, but do imply that there is not a direct tradeoff between cooperation and aggression, and that aggression may be used to regulate foraging when intergroup competition is low. This finding suggests that within-group aggression may not signify within-group conflict, as is often assumed.

INTRODUCTION

The evolution of cooperation is a major focus in behavioral ecology (Dugatkin 1997), with the major theoretical explanations being indirect (Hamilton 1964) and reciprocal (Trivers 1971; Axelrod and Hamilton 1981) fitness benefits. These explanations involve within-group interactions, but another important class of explanations concern interactions between groups in a population. The idea that intergroup competition affects within-group cooperation has arisen in many disciplines, from social psychology (Tajfel 1982; Bornstein 2003) and anthropology (Manson and Wrangham 1991) to economics (Hausken 2000). In brief, intergroup competition increases the net benefit to an individual of cooperating with group members, relative to the benefit of cooperation in the absence of intergroup competition. This explanation is consistent with both individual selection and kin selection (Dugatkin and Reeve 1994; West et al. 2011); it requires that the individuals benefit as well as the group to which they belong, but does not require relatedness among group members to be high (Reeve and Hölldobler 2007). There is abundant and diverse support for this theory: much from non-human vertebrates, e.g. green woodhoopoes *Phoeniculus purpureus* (Radford 2008; Radford 2011), capuchins *Cebus capucinus* (Perry 1996), and chimpanzees, *Pan troglodytes* (Wilson and Wrangham 2003; Muller

and Mitani 2005), but also from bacteria (Brockhurst et al. 2007) and even intraorganismal interactions among sperm (Fisher and Hoekstra 2010). However, the majority of studies focus on humans: intergroup competition may have been important in ancestral human evolution (Bowles 2006; Bowles 2009), and evidence for humans' responses to competing groups is widespread, from laboratory public goods games (Bornstein and Ben-Yossef 1994; Puurtinen and Mappes 2009) and field experiments (Sherif et al. 1954) to anthropological studies (Richerson and Boyd 1999).

Some of the most striking instances of cooperation occur in insect societies (Wilson 1971; Reeve and Hölldobler 2007; Hölldobler and Wilson 2009), for example advanced eusocial species with morphologically distinct queen and worker castes (Bourke 1999). These "superorganism"-like properties (Wilson and Sober 1989; Hölldobler and Wilson 2009) may be due to intergroup competition (Reeve and Hölldobler 2007). In a game theoretic model to explain the evolution of extreme levels of cooperation in advanced insect societies, Reeve and Hölldobler (2007) show that "tug-of-war" competition between groups favors cooperation within groups, and predict that cooperation increases when the number of competing groups increases, the intensity of between-group competition relative to within-group competition increases, and the relatedness between individuals in different groups decreases (summarized in Table 3.1). There is experimental evidence that competition between interspecific colonies affects cooperation in the termites *Cryptotermes secundus* and *C. domesticus* (Korb and Foster 2010), and intergroup competition has been invoked as an explanation for cooperative foraging specialization in queens of *Acromyrmex versicolor* ants (Rissing et al. 1989), but the predictions of Reeve and Hölldobler's

(2007) "nested tug-of-war" model have not been explicitly empirically tested within a social insect species.

In their model, Reeve and Hölldobler (2007) propose that their decision variable f^*, an individual's investment in within-group conflict, provides a metric for "superorganismness". Within-group conflict (equivalently, within-group competition) comprises any behavior that increases an individual's share of resources relative to others' in its group. This is the only decision variable in the model, which thereby assumes that all personal resources not invested in within-group competition are cooperatively contributed to group productivity ($1-f^*$). Cooperation comprises any behavior that increases group productivity relative to other groups; thus, the total cooperative contributions of all group members comprise that group's investment in between-group competition.

However, investment in within-group competition versus cooperation is not necessarily a zero-sum decision: some groups exhibit both high conflict and high cooperation (Queller and Strassmann 2009). In particular, in many cooperatively breeding species, individuals may benefit not by competing over current breeding opportunities, but by waiting in a "reproductive queue" for the opportunity to breed (Wiley and Rabenold 1984; Kokko and Johnstone 1999; Field and Cant 2009). This is the case in vertebrates such as superb fairy wrens *Malurus cyaneus* (Cockburn et al. 2008), and in many primitively social insects such as *Polistes* paper wasps (Cant and Field 2001; Cant et al. 2006) and *Liostenogaster* hover wasps (Field et al. 2006; Field 2008). Thus, a more realistic model of intergroup competition should include a third option of keeping resources. This 3-option model can be generalized to societies in which workers do not

reproduce in the future: in this scenario, one would expect it to predict an optimal investment of zero in keeping resources.

In this study, we extend Reeve and Hölldobler's (2007) model to include the third option of keeping resources, which yields two nested tradeoffs. Firstly, there is a tradeoff between increasing future reproductive opportunities, by conserving their personal resources, and increasing current reproductive opportunities, by investing their personal resources in tug-of-war competition and/or in contributing to group productivity. Secondly, when investing in current reproduction, there is a tradeoff between investing in within-group competition for a share of resources versus cooperating to obtain more resources to be shared, as in the original nested tug-of-war model (Reeve and Hölldobler 2007). We hypothesize that individuals' optimal investments in cooperation and conflict depend on the relative importance of future reproduction and on the nature of the shared resources, and that these factors may interact with intergroup competition. We derive game theoretic "tug-of-war" (Reeve et al. 1998; Reeve and Hölldobler 2007) alternative predictions for the effect of intergroup competition on cooperation and conflict. Using a strong inference approach (Platt 1964), we conduct an empirical test in the primitively social wasp *Polistes dominulus* to falsify these predictions.

MODEL

Constructing the 3-option model

Each individual has a personal energy store of size t, of which it invests an optimal fraction f^* in competing with group members for shared resources (Reeve and Hölldobler 2007). Additionally, each individual contributes an optimal fraction h^* towards group productivity (increasing the size of the shared resources), and keeps the remaining fraction $1-f^*-h^*$ for itself.

We seek the evolutionarily stable pair of strategies f^* and h^*, and start by considering a focal individual who adopts the mutant strategies f and h, instead of f^* and h^*. (We assume that f and h are encoded by a single allele, or pair of tightly linked alleles, although the results of the model are the same if we consider two focal individuals, one carrying a mutant allele for f and the other carrying a mutant allele for h.) The focal individual is in a group of size n, and other group members have a probability r of also carrying the mutant allele(s). The focal's group is in a population of n_g groups, competing in a "tug-of-war" (Reeve et al. 1998; Reeve and Hölldobler 2007) over a resource of value v.

Firstly, we find the fraction of shared resources that the focal individual obtains within its group. This fraction w is determined by the ratio of the focal individual's investment in within-group competition relative to the sum of all group members' competitive investments (where $x=ft$ and $x^*=f^*t$), for a given intensity z of within-group competition (Reeve et al. 1998; Reeve and Hölldobler 2007):

Equation 3.1

$$w = \frac{x^z}{x^z + (n-1)(rx^z + (1-r)x^{*z})}$$

Secondly, we find the fraction of the population resource *v* that the focal individual's group obtains. This is determined by the group members' total contributions *c* to group productivity (where *y=ht*, *y*=h*t*, and *j* is a constant):

Equation 3.2a

$$c = j(y + (n-1)(ry + (1-r)y^*))$$

The total group contribution to group productivity of a group with no mutants is:

Equation 3.2b

$$c^* = jny^*$$

The fraction *b* that the focal individual's group obtains is given by its members' contributions to productivity *c* relative to all other groups' (Reeve and Hölldobler 2007). With probability r_g, individuals in another group possess the mutant allele(s); thus, for an intensity of between-group competition *q*, the focal individual's group obtains a fraction:

Equation 3.3

$$b = \frac{c^q}{c^q + (n_g - 1)(r_g c^q + (1 - r_g)c^{*q})}$$

Thirdly, we construct an expression for the focal individual's fitness. This is given by the amount of resources it obtains in the tug-of-war competition plus the amount of resources it has kept for itself; that is, we incorporate both current and future reproduction. The extent to which an individual values future resources relative to current resources (e.g. due to the probability of surviving to use future resources) is given by the factor v_f:

Equation 3.4

$$vbw + v_f(t - x - y)$$

Finally, to find the strategies f^* and h^* that maximize an individual's fitness, we calculate the partial derivatives of fitness with respect to f and h ($\frac{\partial w}{\partial f}$ and $\frac{\partial w}{\partial h}$). At the fitness maximum, both of these partial derivatives are equal to zero, $f=f^*$, and $h=h^*$. We thus simultaneously solve these expressions for f^* and h^*, and verify that they are fitness maxima by checking that the second derivatives are negative.

We obtain the following stable solutions for the investment in within-group competition, contribution, and keeping resources respectively:

Equation 3.5

$$f^* = \frac{(n-1)(1-r)zv}{n^2 n_g t v_f}$$

$$h^* = \frac{(n_g - 1)(1 - r_g)(r(n-1)+1)qv}{n^2 {n_g}^2 t v_f}$$

$$1 - h^* - f^* = \frac{n_g(n-1)(1-r)zv + (n_g - 1)(r_g - 1)(r(n-1)+1)qv + n^2 {n_g}^2 t v_f}{n^2 {n_g}^2 t v_f}$$

We can thus predict how a change in any parameter (n, n_g, r, r_g, z, q, v, v_f and t) affects an individual's evolutionarily stable investments in f^*, h^* and $1-f^*-h^*$ (Table 3.1).

Resources proportional to population size

In the above model, the population resource over which groups are competing has a fixed value v. However, v may vary with the size of the population, for example when individuals are in an ideal free distribution (Kennedy and Gray 1993). In this case, we have:

Equation 3.6

$$v_p = kn_g n$$

where k is a constant. We substitute this expression for v into the fitness function, and repeat the steps above in order to obtain the following evolutionarily stable investments in within-group competition, cooperation, and keeping resources:

Equation 3.7

$$f_p^* = \frac{(n-1)(1-r)kz}{ntv_f}$$

$$h_p^* = \frac{(n_g-1)(1-r_g)(r(n-1)+1)kq}{nn_g tv_f}$$

$$1 - f_p^* - h_p^* = \frac{n_g(n-1)(r-1)kz + (n_g-1)(r_g-1)(r(n-1)+1)kq + nn_g tv_f}{nn_g tv_f}$$

Again, we can predict how a change in any of the above parameters changes individuals' optimal investments in competition, cooperation and keeping when the population resource is a function of the population size (Table 3.1).

Reeve and Hölldobler's (2007) 2-option model

In the nested tug-of-war model (Reeve and Hölldobler 2007), the only decision variable is *f**, an individual's investment in within-group competition; thus an individual contributes 1-*f** to group productivity. For comparison, using the notation above, these solutions in the Reeve and Hölldobler (2007) model are:

Equation 3.8

$$f_{RH}^{*} = \frac{(n-1)(r-1)n_g z}{(n_g-1)(r_g-1)(r(n-1)+1)q + (n-1)(r-1)n_g z}$$

$$1 - f_{RH}^{*} = \frac{(n_g-1)(r_g-1)(r(n-1)+1)q}{(n_g-1)(r_g-1)(r(n-1)+1)q + (n-1)(r-1)n_g z}$$

As for the two versions of the 3-option model (fixed *v*, and *v* proportional to population size), the effect on these strategies of changing the different parameters (Reeve and Hölldobler 2007) is summarized in Table 3.1.

Table 3.1. Comparison of predictions made by the different models of intergroup competition: an increase in each of the parameters in the left-hand column results in an increase (↑), decrease (↓), or no change (0) in the evolutionarily stable strategies f^*, h^* and $1-f^*-h^*$.
n_g = number of competing groups; n = number of individuals in a group; r = within-group relatedness; r_g = between-group relatedness; z = intensity of within-group competition; q=intensity of between-group competition; t = each individual's starting amount of resources.

Increase in…	Investment in tug-of-war (f^*)			Cooperative contribution (h^*)			Kept for self ($1-f^*-h^*$)		
	Reeve & Hölldobler	3 options		Reeve & Hölldobler	3 options		Reeve & Hölldobler	3 options	
		v=constant	$v=kn_gn$		v=constant	$v=kn_gn$		v=constant	$v=kn_gn$
n_g	↓	↓	0	↑	↓	↑	n/a	↑	↓
n	↑	↓	↑	↓	↓	↓	n/a	↑	↑ or ↓ [1]
r	↓	↓	↓	↑	↑	↑	n/a	↑ or ↓ [2]	↑ or ↓ [1]
r_g	↑	0	0	↓	↓	↓	n/a	↑	↑
z	↑	↑	↑	↓	0	0	n/a	↓	↓
q	↓	0	0	↑	↑	↑	n/a	↓	↓
t	0	↓	↓	0	↓	↓	n/a	↑	↑
v	n/a	↑	n/a	n/a	↑	n/a	n/a	↓	n/a
v_f	n/a	↓	↓	n/a	↓	↓	n/a	↑	↑

[1] Whether this is an increase or decrease depends on the relative values of n_g, n, r, r_g, z and q.
[2] Whether this is an increase or decrease depends on the relative values of n_g, r_g, z and q.

Comparing the models' predictions

There are thus three sets of testable predictions for how groups will respond to changes in each parameter (Table 3.1); we focus here on those concerning changes in between-group competition. When the number of competing groups n_g increases: (1) both the Reeve and Hölldobler (2007) and fixed-*v* models predict a decrease in within-group competition, but the population-*v* model predicts no change; (2) both the Reeve and Hölldobler (2007) and population-*v* models predict an increase in within-group cooperation, but the fixed-*v* model predicts a decrease; (3) the fixed-*v* model predicts an increase in the amount of personal resources kept for oneself, but the population-*v* model predicts a decrease. Thus, for any change in n_g, each model predicts a different relationship between the changes in individuals' investments in within-group competition, cooperation, and keeping resources. We experimentally tested these predictions about the absolute changes in these investments, and the relationships between them, in the paper wasp *Polistes dominulus*, by manipulating the number of competing nests in the field and the laboratory.

METHODS

Study species

The primitively eusocial wasp *Polistes dominulus* is a model system for studying cooperation and conflict (Reeve 2001; Field and Cant 2006), given its flexible social structure (Reeve 1991)

and easily observable cooperative and selfish behaviors: for example, foraging is costly to the forager but benefits all other group members (cooperative), and aggression towards wasps of adjacent dominance rank may increase the aggressor's chances of becoming more dominant (selfish). In addition, this species is especially suitable for this study, for two reasons: firstly, conserving resources for future reproduction is an important component of fitness in this species (Leadbeater et al. 2011); and secondly, nests occur in large populations where wasps frequently encounter conspecifics from other nests (Zanette and Field 2011), and thus are likely to experience intergroup competition.

In temperate *Polistes* species, such as *P. dominulus*, mated females establish nests in the spring, either solitarily or in multiple-foundress associations (Reeve 1991). In the latter case, the dominant foundress lays eggs, while the subordinates wait in a "reproductive queue" to inherit the breeding position (Field and Cant 2006; Field and Cant 2009). An individual's rank in the queue, and thus her probability of future direct fitness benefits, affects her optimal levels of within-group competition to increase her dominance rank (Cant et al. 2006) and cooperative contribution to group productivity (Cant and Field 2001). Additionally, some foundresses gain direct fitness by adopting other nests, and those following this "sit-and-wait" tactic conserve more energy than do other foundresses (Starks 1998).

The first adults to emerge tend to become workers, while gynes emerge later in the season (Reeve 1991). However, there are no morphological differences between gynes and workers (Reeve 1991), and some early workers leave the nest in order to attempt to become foundresses the next spring (Reeve et al. 1998) and tend to be more selfish, foraging less and spending less

time active (Tibbetts 2007). Thus, the trade-off between investing in current fitness and future fitness applies to workers as well as foundresses.

Field experiment

Manipulation

We experimentally manipulated intergroup competition by transplanting 32 *P. dominulus* colonies. All nests were originally found on and transplanted between buildings of the Liddell Field Station near Ithaca, New York, and were in the early worker phase (late June – early July 2007); we transplanted nests randomly with respect to size and original location. Post-transplant locations were grossly categorized into high and low nest density (high and low intergroup competition respectively): in the former category, we transplanted nests close together, and left non-experimental colonies on the buildings, while in the latter, we removed all non-experimental colonies, and transplanted colonies further apart (Figure 3.1a). However, distances between nests varied within each category, and thus we analyzed nearest neighbor distance as a continuous variable. (Post-transplant nearest neighbor distances were within the range we observed for pre-transplant nests: see appendix.) We also removed all adults (foundresses and workers) already on the nest, with the result that any individuals on the post-transplant nests would have emerged in that location and not have experienced the pre-transplant location. None of these nests were adopted by other foundresses (all foundresses in the population had been marked earlier in the season).

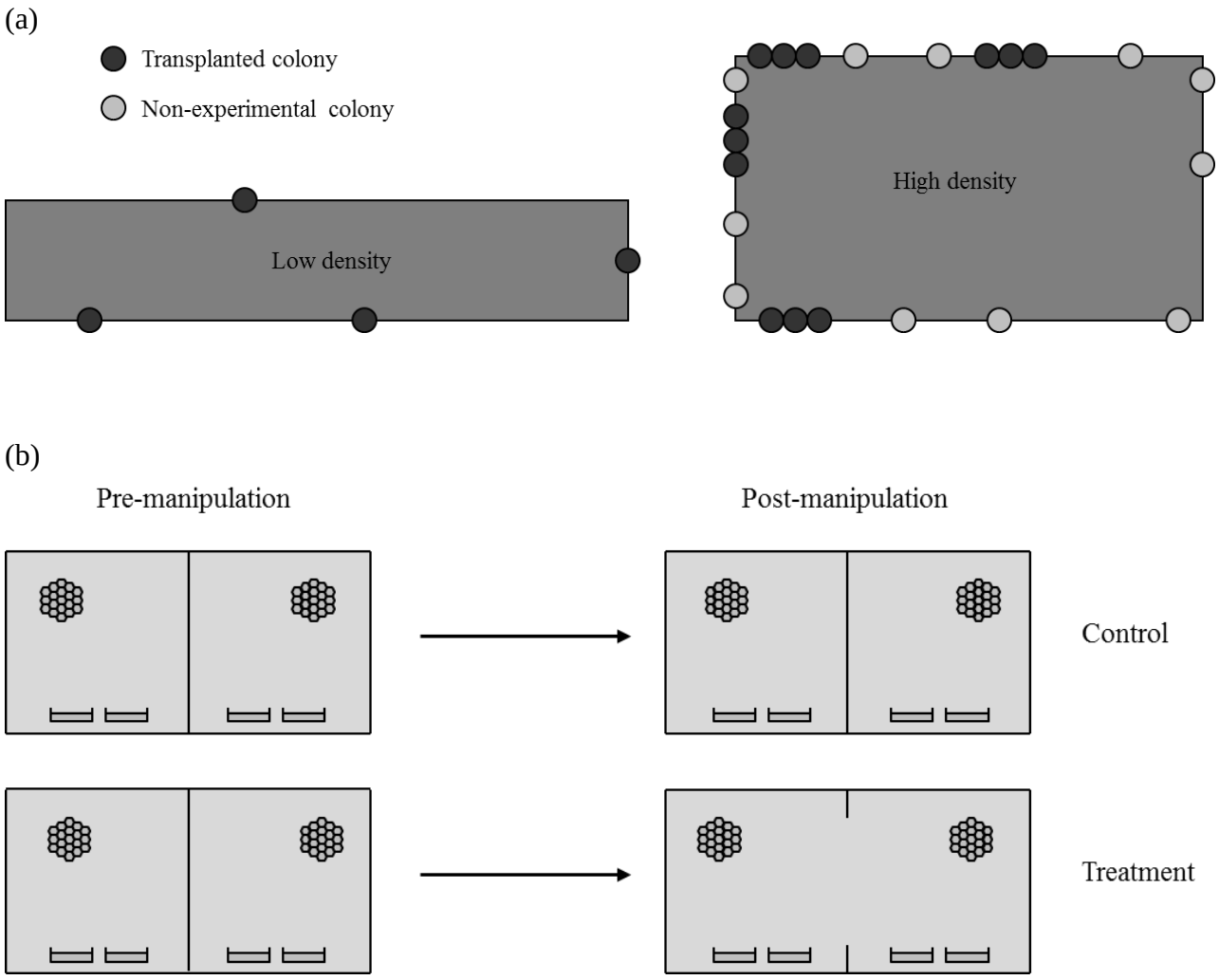


Figure 3.1. Set-up of field and lab experiments. (a) In the field, we transplanted 8 nests to low density areas, where we removed all non-experimental colonies, and 16 nests to high density areas; in the latter, non-experimental colonies remained on the buildings, and we transplanted experimental colonies in clusters. (b) In the lab, we put each nest in its own box with food and water. In 4 treatment pairs, we removed the partition separating the two colonies (exposure to intergroup competition), while in 4 control pairs, the partition remained throughout the experiment (no intergroup competition).

Observations and statistical analyses

Starting one week after the transplants, after new workers had begun to emerge, we recorded at least two hours of video observations of each nest (n=23, excluding nests that were depredated or otherwise failed after the transplants). We scored all aggressive behaviors (darts and lunges; no other aggressive behaviors identified), and calculated the rates per individual per hour. We used the rate of nest departures per individual per hour as a proxy for cooperative foraging effort, given that leaving the nest is costly (Cant and Field 2001). We also recorded nest activity levels every five minutes as the percentage of wasps that were active.

To ensure that the residuals in the statistical models were normally distributed, we transformed aggressive acts and departures as $\log_{10}(1+\text{rate})$ (Tibbetts and Reeve 2000), and $\log_{10}$-transformed the percentage of active wasps and nearest neighbor distances. Neither nest size (at the time of transplant or at the time of observation) nor the time between transplant and observation was correlated with nearest neighbor distance (all p>0.2). Thus, we excluded nest size and time from the below analyses, and performed partial Pearson correlations controlling for temperature.

Laboratory experiment

Manipulation

We collected 16 early worker phase *P. dominulus* nests from Liddell Field Station buildings, and transplanted them into the laboratory in July 2008. We gave every wasp a nest-specific paint

mark on her thorax, and housed each nest individually in a cardboard box, approximately 900 cm^3, with a transparent plastic front for viewing. Each nest had access to construction paper for nest-building, *ad libitum* water and honey-water mixture, and a fixed number of mealworms proportional to the size of the nest. We randomly assigned nests to pairs, and randomly assigned 4 pairs to a control group and 4 pairs to a treatment group. In the experimental manipulation, we cut down the cardboard wall separating the two colonies in each pair of treatment nests; for the control nests, we cut and immediately replaced the wall (Figure 3.1b). Thus, after the manipulation, wasps on a control nest remained in an isolated box, while wasps on a treatment nest were potentially in competition with the other treatment nest in the pair.

Observations and statistical analyses

We recorded two hours of video observations of each nest before and after the experimental manipulation. One nest in the control treatment failed, and thus we had n=7 control nests and n=8 treatment nests. We scored activity levels and aggressive behaviors as in the field experiment. Given that wasps in the lab frequently left the nest for a few seconds without attempting to bring back food (J. L. Barker, personal observation), we did not use departure rate as a measure of foraging effort, as we did in the field experiment. Instead, we used two alternative measures of foraging: (1) rate of returns to the nest (per individual per hour) with visible food items (caterpillar or nectar droplet), and (2) proportion of wasps off the nest, given that individuals not on the nest tended to cluster around the food (J. L. Barker, personal observation), and that in many cases we could not detect whether a wasp was returning with food or not. All nests in the lab experienced the same constant temperature, and we recorded videos of

all nests synchronously; thus we exclude temperature and time since transplant from the analyses.

We examined whether behavior on each nest differed after the experimental manipulation, using t-tests for normally distributed data and Wilcoxon rank sum tests for non-normally distributed data. Firstly, we compared pre- and post-manipulation behavior within a given nest (paired tests). Secondly, we calculated the percentage changes in aggression, activity, wasps off the nest and returns with food by subtracting the pre-manipulation value from the post-manipulation value for each nest, and finding this as a percentage of the pre-manipulation value. We determined whether these changes were significant (one-sample tests), and whether they differed between treatments and controls (unpaired tests).

Additionally, given that group size may affect investments in within-group cooperation and conflict (Table 3.1), we investigated whether the number of wasps on the nest affected the percentage change in behaviors, using Pearson correlations for data whose residuals were normally distributed and Spearman rank correlations for those with non-normal residuals. We also tested whether the change in each behavior was correlated with changes in the other behaviors, since the different models predict different relationships between these changes (Table 3.1). We used Pearson correlations for data whose residuals were normally distributed and Spearman rank correlations for those with non-normal residuals, and Fisher's *r*-to-*z* transformation to determine whether these correlations were significantly different between treatments and controls.

RESULTS

Field experiment

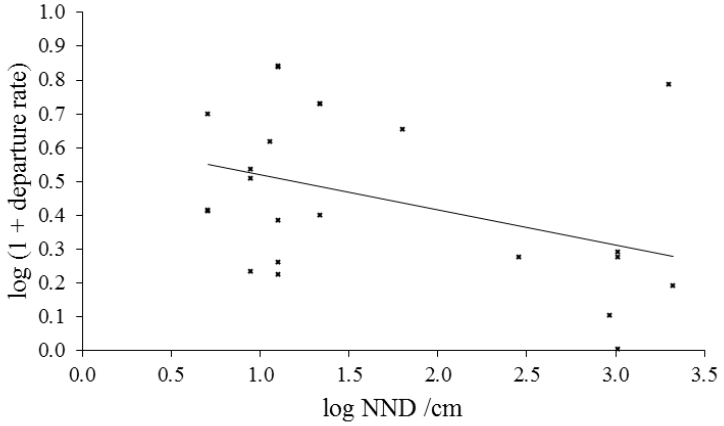
Departure rates, aggression rates, and the proportion of active wasps were all negatively correlated with nearest neighbor distances ($\log_{10}$-transformed data, partial correlations controlling for temperature; departure rates: r= -0.4368, p= 0.0299; aggression rates: r= -0.5193, p= 0.0066; proportion of active wasps: r= -0.4778, p= 0.0150). That is, when nests were closer together, wasps were more active, departed more frequently, and were more aggressive to nestmates (Figure 3.2).

Laboratory experiment

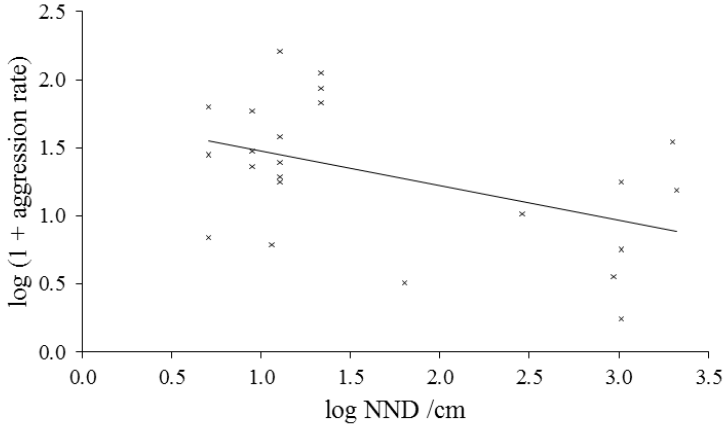
Differences before and after manipulation

There were no significant differences between pre- and post-manipulation control or treatment nests in (i) aggression rate, (ii) proportion of active wasps, (iii) proportion of wasps off the nest, or (iv) rate of returning to nest with food items (paired t and Wilcoxon rank sum tests; all p>0.1). None of the percentage changes in each of these behaviors was significantly different from zero (one-sample t and Wilcoxon rank sum tests; all p>0.1; Figure 3.3). These changes were not significantly different between treatments and controls (unpaired t and Wilcoxon rank sum tests; all p>0.1).

(a)



(b)



(c)

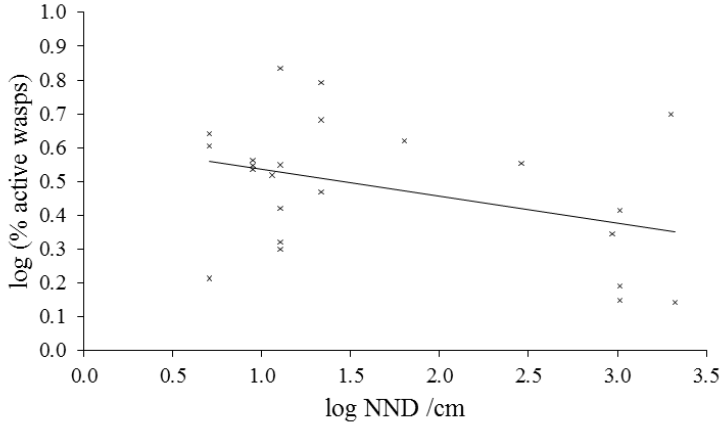


Figure 3.2. Nest proximity had a significantly negative effect on the (a) rate of departures (r= -0.4368, p= 0.0299), (b) rate of aggression (r= -0.5193, p= 0.0066), and (c) percentage of wasps that were active(r= -0.4778, p= 0.0150). Nest proximity is given by nearest neighbor distance (NND), and rates are calculated per hour per individual on the nest.

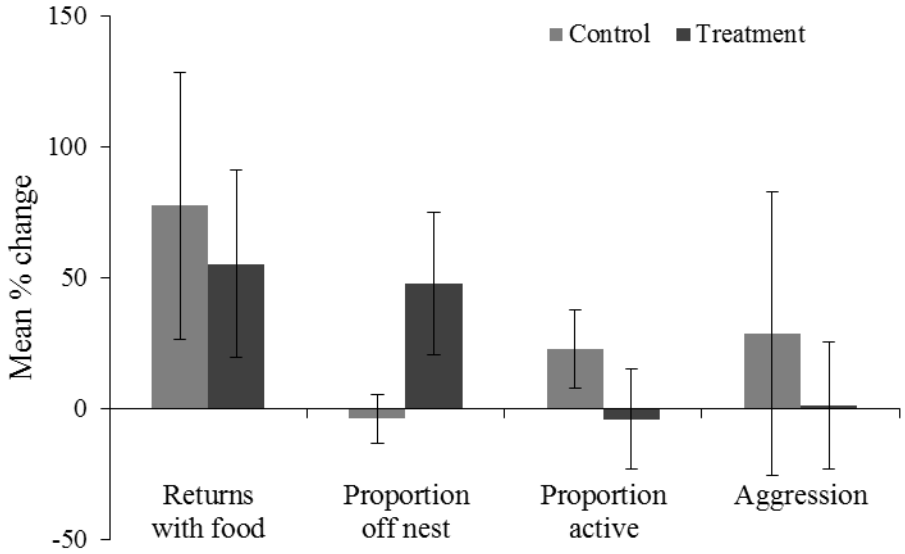


Figure 3.3. There were no significant changes in any behaviors during the experiment, and no significant differences between control and treatment nests. Changes are given as the difference between the post-manipulation and pre-manipulation value as a percentage of the pre-manipulation value.

Nest size

Nest size was not significantly correlated with changes in (i) aggression rate, (ii) proportion of active wasps, (iii) proportion of wasps off the nest, or (iv) rate of returning to nest with food items, in either treatments or controls (Pearson correlations; all $p>0.15$). In post-manipulation treatment nests, the relative difference in size between focal and competing nests (calculated as [size of focal minus size of competitor] as a percentage of the size of the focal nest) was non-significantly correlated with the change in proportion of wasps off the nest (Spearman rank correlation: $\rho=0.6976$, $p=0.0544$), but not with the rate of returns with food, rate of aggression, or proportion of active wasps (all $p>0.4$).

Partial correlations between changes in aggression, foraging and activity (Table 3.2)

The change in activity was negatively correlated with the change in aggression in control nests, controlling for either returns with food ($r=-0.9512$, $p<0.0001$) or proportion of wasps off the nest ($\rho=-0.7749$, $p=0.0142$). In treatments, however, the change in activity was positively correlated with the change in aggression (controlling for returns with food: $r=0.7236$, $p=0.0191$; non-significant when controlling for proportion off nest: $r=0.5489$, $p=0.1421$). The correlations in treatments were significantly different to the correlations in controls (controlling for returns with food: $z=-4.11$, $p<0.0001$; controlling for proportion off nest: $z=-2.46$, $p=0.0139$).

The change in activity was positively correlated with the change in returns with food, controlling for aggression, in controls ($r= 0.9717$, $p<0.0001$) and non-significantly in treatments ($r=0.6259$,

Table 3.2. Partial correlations between changes in behaviors in control and treatment colonies in the lab (Pearson correlations for variables with normally distributed residuals; otherwise, Spearman rank correlations). Fisher's *r*-to-*z* transformation tests whether the correlation coefficients for controls and treatments are significantly different (n.s. = non-significant).

Partial correlation between changes in:		**Controlling for change in:**	**Control**	**Treatment**	**Different in control and treatment?**
Activity	Aggression	Returns with food	Negative r=-0.9512 p<0.0001	Positive r=0.7236 p=0.0191	Yes z=-4.11 p<0.0001
Activity	Aggression	Proportion off nest	Negative ρ=-0.7749 p=0.0142	n.s. r=0.5489 p=0.1421	Yes z=-2.46 p=0.0139
Aggression	Returns with food	Activity	Positive r=0.9495 p<0.0001	n.s. r=-0.4168 p=0.3053	Yes z=3.39 p=0.0007
Aggression	Proportion off nest	Activity	n.s. ρ=0.6965 p=0.0522	n.s. r=-0.1520 p=0.7309	n.s. z=1.51 p=0.131
Activity	Returns with food	Aggression	Positive r= 0.9717 p<0.0001	n.s. r=0.6259 p=0.0727	Yes z=2.07 p=0.0385
Activity	Proportion off nest	Aggression	n.s. r=0.1023 p=0.8370	Positive r=0.7356 p=0.0152	n.s. z=-1.25 p=0.2113

p=0.0727); these correlations were significantly different (z=2.07, p=0.0385). The change in activity was also positively correlated with the change in the proportion of wasps off the nest, controlling for aggression (non-significant in controls: r=0.1023, p=0.8370; treatments: r=0.7356, p=0.0152), but there was no significant difference between controls and treatments (z=-1.25, p=0.2113).

The change in aggression was positively correlated in controls with the changes in returns with food (r=0.9495, p<0.0001) and proportion of wasps off the nest (non-significant: ρ=0.6965, p=0.0522), controlling for aggression. These correlations were non-significantly negative in treatments (returns with food: r=-0.4168, p=0.3053; proportion of wasps off the nest: r=-0.1520, p=0.7309). The correlations involving returns with food were significantly different in treatments and controls (z=3.39, p=0.0007) but those involving the proportion of wasps off the nest were not (z=1.51, p=0.131).

DISCUSSION

Theoretical predictions and empirical results

The game theoretic models give three alternative sets of predictions about the changes in wasps' cooperation and conflict with changes in between-group competition. When the number of competing groups, n_g, increases, as in our experimental manipulations, Reeve and Hölldobler's (2007) nested tug-of-war model predicts that cooperation increases and within-group competition

decreases, the 3-option fixed-*v* model predicts that both cooperation and within-group competition decrease, and the 3-option population-*v* model predicts that cooperation increases and aggression does not change. Our empirical results do not fully support any of these predictions: in the field study, on-nest aggression, foraging and nest activity increased when nests were transplanted closer together; while in the lab study, there was no change in aggression, foraging or activity when colonies were exposed to a competing group. However, correlations between changes in aggression, activity and foraging in the lab suggest that there may be effects of intergroup competition not predicted by the models.

Increases in both on-nest aggression and foraging in the transplanted nests in the field experiment suggests that the simple 2-option model (Reeve and Hölldobler 2007) does not apply to *P. dominulus*. Indeed, this finding is corroborated by evidence that *Polistes* foundresses and workers do take into account future reproductive options, and are not simply making decisions concerned with increasing current reproductive opportunities by investing in within-group cooperation and conflict. Firstly, individuals vary their investments in helping and aggression based on their probability of future reproduction, as determined by rank (Cant and Field 2001; Cant et al. 2006). Secondly, both foundresses (Starks 1998) and workers (Reeve et al. 1998) may adopt alternative reproductive strategies that maximize the probability of reproducing elsewhere; for workers, this is associated with conserving energy and going into early diapause (Tibbetts 2007). In contrast, in the lab experiment presented here, there were no changes in aggression or foraging when colonies were exposed to competing nests. Three alternative explanations for this result are as follows. Firstly, the presence of a single competing colony may not be enough to cause changes; however, this is unlikely, because there were other differences between treatment

and control colonies (see "Stimulation of foraging and the role of aggression" below). Secondly, although foraging is costly in the field (O'Donnell and Jeanne 1992) and thus a good measure of cooperation, this is not the case in the lab, where food was readily available close to each nest. Thirdly, wasps in the lab may have assessed their options for future reproduction differently than those in the field, for example because there were no suitable hibernacula for winter diapause in the lab enclosures, or because queens were still present on the lab nests but removed from the field nests.

The field results not only fail to support the 2-option model's predictions (Reeve and Hölldobler 2007), but also do not support those from either of the 3-option models presented here. One explanation could be that food was distributed unevenly in our field population, such that the nests we transplanted to be closer together were in an area with more food, causing more foraging and more activity. If this were the case, it would not be surprising that the data do not support the 3-option models' predictions, given that these predictions are sensitive to *v*, the value of the resource shared among groups. An alternative explanation is that the increase in nest departures when nests were closer together may not have corresponded to an increase in foraging, but rather may have indicated an increase in wasps investigating nearby colonies for possible usurpations. A third explanation is that the aggression we observed does not function to increase the size of wasps' current share of resources. One possible function of aggression is to deter non-nestmate intruders. When nests are closer together, they may be at greater risk of usurpation or conspecific nest intrusion to steal larvae (Reeve 1991); this costly scenario may select for a shift in the threshold of aggression towards nestmates (Reeve 1989; Starks et al.

1998). An alternative function of aggression may be to regulate foraging or activity on the nest, as suggested by the wasps' behavior in the lab.

Stimulation of foraging and the role of aggression

There was a positive partial correlation between the change in activity and the change in foraging, controlling for the change in aggression, in both treatments and controls in the lab, which suggests that regardless of intergroup competition, higher activity is associated with higher foraging, as in *P. fuscatus* (Reeve and Gamboa 1987). However, there were differences between treatments and controls in other partial correlations between activity, foraging and aggression, which suggests that the experimental manipulation in the lab did indeed have an effect (see "Theoretical predictions and empirical results" above). In controls, aggression and foraging changed in the same direction, controlling for the change in activity, while this was not the case for treatments. Aggression and activity, controlling for the change in foraging, changed in parallel in treatments but in opposite directions in controls. This suggests a different role for aggression in treatments than in controls.

The basis of the 2-option nested tug-of-war model (Reeve and Hölldobler 2007) is that intergroup competition changes the benefits to an individual of cooperatively contributing to group resources, as when *P. dominulus* workers forage for food to be shared with adult and larval nestmates. The positive correlation between aggression and foraging in control nests in the lab suggests that in the absence of intergroup competition, aggression may be involved in stimulating foraging: all else equal, group members face a "volunteer's dilemma" where they

may do better by being lazy and letting others do the work (Field and Cant 2006; Tibbetts 2007). In contrast, when there are other groups competing over a shared resource, individuals may benefit by voluntarily going foraging. In treatment nests, i.e. those exposed to a competing nest, aggression may instead be directed towards increasing nest activity, as is known to be the case in *P. fuscatus* (Sumana and Starks 2004), and similar to naked mole-rats shoving lazy workers (Reeve 1992). Activity regulation may be carried out by the queen, as in *P. fuscatus* (Reeve and Gamboa 1987), or by workers, as in *P. versicolor* (De Souza and Prezoto 2012), *P. instabilis* and *P. dominulus* (Jha et al. 2006). Thus, aggression may not be a good measure of within-group competition over resource shares in *P. dominulus*. Likewise, in both *Ropalidia marginata* (Bruyndonckx et al. 2006; Lamba et al. 2008) and *Polybia occidentalis* (O'Donnell 2001; O'Donnell 2006), aggression is used to stimulate foraging without being involved in within-group reproductive conflict. This may explain why the empirical results do not fully support any of the models' alternative predictions about the changes in within-group competition.

Implications and extensions

Although many studies of different taxa support the prediction that intergroup competition is associated with within-group cooperation (Bornstein et al. 1990; Manson and Wrangham 1991; Brockhurst et al. 2007; Fisher and Hoekstra 2010; Radford 2011), there is also evidence from non-human primates that it can be associated with within-group aggression. For example, there was no relationship between within-group affiliative grooming behavior and between-group conflict in vervets *Cercopithecus aethiops* (Cheney 1992), and within-group aggression is associated with between-group aggression in two species of macaque (*Macaca radiata*: Cooper

et al. 2004; *M. silenus*: Zinner et al. 2001). Polizzi di Sorrentino et al. (2011) tested two hypotheses for captive capuchin (*Cebus apella*) groups' responses to between-group competition: increased cooperation and increased "induced tension". Their finding of increased within-group aggression and no change in within-group affiliative behavior supports the latter hypothesis and not the former; the authors suggest that within-group aggression may be a type of policing to maintain within-group dominance hierarchies following intergroup conflict (Polizzi di Sorrentino et al. 2011).

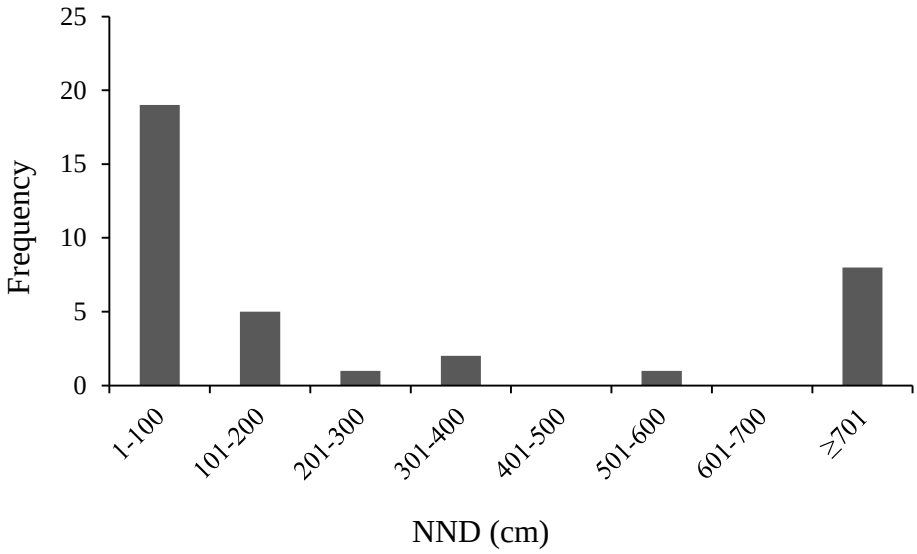
Many social taxa have easily quantifiable cooperative behaviors, such as grooming in primates (Newton-Fisher and Lee 2011) and foraging in social insects (Cant and Field 2001), but identifying behavior that contributes to within-group resource competition may not be so easy. Thus, future studies should determine how to assess both within-group conflict and the extent to which individuals are conserving resources for future reproduction. In addition, future theoretical and empirical work should investigate the effect of asymmetries in group size. The result here that when a focal nest was larger relative to its competing nest, there was a non-significantly larger change in the proportion of wasps off the focal nest, suggests that group size may have an effect on cooperation and intergroup competition, as it does in capuchins *Cebus capucinus* (Crofoot and Gilby 2011) and marmosets *Callithrix kuhli* (Schaffner and French 1997). Further theoretical work should also explore other methods of modeling the 3-option scenario, beyond the tradeoff between current and future reproduction presented here. One potential approach is, rather than constraining each option to benefit either the individual or the group, as in the current models, to weight each option according to the extent to which it benefits the individual and the group, and investigate how these weightings affect individuals' optimal investments in each.

In sum, the implications of this study are as follows. Firstly, there was not a direct tradeoff between foraging and aggression. This may be because individuals face an additional tradeoff between investing in current versus future reproduction; this is beyond the scope of the present study's results, but regardless points to the importance of not assuming that all energy not invested in conflict is invested in cooperation (Queller and Strassmann 2009). Secondly, we must be cautious about interpreting aggressive behavior: it may be implicated in reproductive conflict, but this is not necessarily the case. Thirdly, the effect of intergroup competition may be more subtle than a simple increase in within-group cooperation or conflict, as demonstrated by the correlations in the lab results presented here. For example, people respond to the presence of competing groups even when this does not affect their incentives for cooperation (Tan and Bolle 2007), analogous to social facilitation (Zajonc 1965) at a group level. Future work should investigate why different groups respond in different ways. Finally, if intergroup competition does affect within-group behavior, this raises the intriguing possibility that group members could manipulate such an effect to their own advantage, for example in order to stimulate cooperation (Barclay and Benard 2011).

APPENDIX

Post-transplant nearest neighbor distances were within the range we observed for pre-transplant nests (Figure S3.1).

(a)



(b)

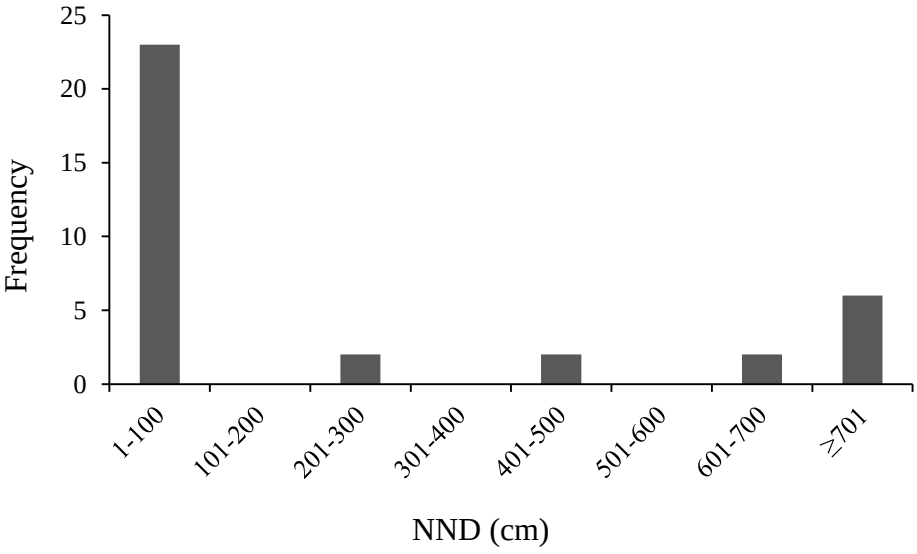


Figure S3.1. Nearest neighbor distances of nests at the field site (a) before and (b) after the experimental transplant.

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CHAPTER 4

ASYMMETRIES IN A SOCIAL GROUP: DIVISION OF LABOR AND INTERGROUP COMPETITION

Jessica L. Barker, Kevin J. Loope and H. Kern Reeve

A major challenge in behavioral ecology is to explain cooperation among individuals in social groups. Competition among groups provides one explanation for within-group cooperative behavior, but existing models of intergroup competition have failed to account for the fact that not all group members invest in cooperation. Social groups are often characterized by competitive and relatedness asymmetries among group members, and here we present a game theoretic model of cooperation that incorporates both within-group variation and between-group competition. In the model, each group contains two roles; a player's strategy dictates its behavior in each role, and individuals in each role make simultaneous, coevolving decisions. When relatedness, relative competitive efficiency and the number of individuals are allowed to vary between roles, the model predicts that individuals in one role ("workers") predominantly contribute to group resources, while an individual in the other role (the "queen") generally gains the larger share of these resources. This effect is greatest when there is a greater asymmetry in competitive efficiency between the roles, when individuals in the worker-like role are more related to each other than they are to the individual in the queen-like role, and when there are more workers in the group. The model also predicts that the effect of intergroup competition on both roles' cooperation is only noticeable when there are few competing groups. These predictions are consistent with observations in many social groups (e.g. hymenopteran societies

with a single queen, many workers, and caste dimorphism), but need to be explicitly tested.

INTRODUCTION

The balance between cooperation and conflict within social groups, and concomitantly the degree of equitable resource division, is a major area of research in behavioral ecology (Owens 2006; West et al. 2007; Korb and Heinze 2008; Clutton-Brock et al. 2009; Cant 2012). In particular, much research has focused on explaining the origin and maintenance of eusociality in insects (Wilson 1971; Reeve 2001; Ratnieks and Wenseleers 2007; Gadagkar 2009; Ratnieks and Helanterä 2009): many insect societies exhibit such high levels of cooperation and low levels of conflict that they function as "superorganisms" (Wilson and Sober 1989; Reeve and Hölldobler 2007; Hölldobler and Wilson 2009) whose evolution is analogous to that of a multicellular organism (Maynard Smith and Szathmáry 1995; Michod and Roze 2001; Queller and Strassmann 2009). Insect societies vary in social complexity (Bourke 1999) and form a continuum of sociality with other taxa (Sherman et al. 1995). However, individuals across the sociality continuum face a common tradeoff: how much to invest in obtaining a larger share of the group's resources for personal reproduction, at the expense of investing in cooperative production of more resources that are shared among all group members (Reeve et al. 1998).

One hypothesis to explain this balance between cooperation and conflict within groups concerns the effect of conflict between groups; that is, when intergroup competition is higher, a group member benefits by investing more in within-group cooperation (Rabbie and Wilkens 1971;

Bornstein et al. 1990; Bornstein 2003; Reeve and Hölldobler 2007). This is because within-group cooperation allows a group to compete more effectively against other groups: intergroup competition increases the net benefit to an individual of within-group cooperation (Reeve and Hölldobler 2007). Thus, this hypothesis (1) is consistent with individual selection, since multilevel trait-group selection models are equivalent to individual selection models (Dugatkin and Reeve 1994; West et al. 2011); and (2) does not preclude the role of relatedness, but rather shows how within-group cooperation can be favored even when within-group relatedness is low (Korb and Heinze 2004; Reeve and Hölldobler 2007). There is wide support for the intergroup competition hypothesis, primarily from vertebrates including humans (Sherif et al. 1954; Bornstein and Ben-Yossef 1994; Bornstein et al. 2002; Bowles 2009; Puurtinen and Mappes 2009; Gneezy and Fessler 2012), other primates (chimpanzees, *Pan troglodytes*: Wilson and Wrangham 2003; Muller and Mitani 2005), and birds (green woodhoopoes, *Phoeniculus purpureus*: Radford 2008; Radford 2011), in addition to intraorganismal intergroup conflict among mouse sperm (*Peromyscus* spp.: Fisher and Hoekstra 2010). Intergroup competition has also been proposed as a factor selecting for superorganism-like insect societies (Reeve and Hölldobler 2007), although there are few tests of this hypothesis in social invertebrates (but see Rissing et al. 1989; Korb and Foster 2010).

While the intergroup competition hypothesis undoubtedly explains many instances of within-group cooperation, it does not take into account differences among group members. Firstly, there may be consistent individual variation in cooperative behavior (Bergmüller et al. 2010; McNamara and Leimar 2010), as in meerkats, *Suricata suricatta* (English et al. 2010); and lions, *Panthera leo* (Heinsohn and Packer 1995). Secondly, group members may vary their cooperation

depending on their relatedness to the recipients, for example in paper wasps, *Polistes dominulus* (Queller et al. 2000; but see Leadbeater et al. 2010); slime molds, *Dictyostelium discoideum* (Strassmann et al. 2000); and bee-eaters, *Merops bullockoides* (Emlen and Wrege 1988). Thirdly, the costs and benefits of cooperation may differ for different group members: reasons for such differences include variation in individuals' "power" to respond to conflicts of interest (Beekman et al. 2003; Beekman and Ratnieks 2003) and in the probability of obtaining a breeding opportunity (Cant and Field 2001; Cant and Field 2005; Field et al. 2006). Insect societies in particular exhibit striking within-group division of cooperative labor (Reeve and Keller 2001; Field and Cant 2006), for example between queens and workers.

In order to understand fully the effect of intergroup competition on within-group cooperation, it is therefore crucial to incorporate within-group variation. Here, we present a game theoretic model in which group members adopt one of two roles, where individuals in one role may differ in relatedness and relative competitive efficiency ("power", *sensu* Beekman et al. 2003; Beekman and Ratnieks 2003) to other group members. Individuals in each role make decisions simultaneously: that is, their behaviors coevolve. We use Reeve and Hölldobler's (2007) game theoretic nested tug-of-war framework, and examine how within-group asymmetries interact with intergroup competition to affect within-group cooperation and resource division.

MODEL

Structure of the model

Each member of a social group adopts one of two roles, with n_1 individuals in Role 1 and n_2 individuals in Role 2. A group member plays the optimal strategy x^* of selfishly investing effort in acquiring a share of the group's resources, which translate into reproductive opportunities (we use "share of reproduction" and "within-group share of resources" interchangeably), at the expense of cooperatively contributing $1-x^*$ to the total amount of resources shared by all group members (that is, the "group's productivity", or the "group's share"; we use these terms interchangeably). An individual playing this strategy plays x_1^* when in Role 1 and x_2^* in Role 2. Likewise, an individual adopting the mutant strategy x plays x_1 in Role 1 and x_2 in Role 2. A strategy is therefore a rule telling an individual which pair of role-specific sub-strategies to adopt, i.e. x_1^* or x_2^* versus x_1 or x_2.

Here we take a neighbor-modulated fitness approach to modeling relatedness within groups (Hamilton 1964; Wenseleers et al. 2010). We consider the invasion of a rare mutant allele x in a population of individuals playing x^*. If the mutant allele causing an individual to play x instead of x^* is in an individual in Role 1, this allele will be found in another Role 1 player with probability r_{11}, and in a Role 2 individual with probability r_{12}. Likewise, if this mutant allele is in a focal Role 2 player, it will be found in another individual in Role 2 with probability r_{22}, and in a Role 1 player with probability r_{21}.

In order to find the evolutionarily stable values of x_1*and x_2*, we consider a focal mutant individual's expected fitness *w* across the two roles: w_1 and w_2 for Role 1 and Role 2 respectively. We use Reeve and Hölldobler's (2007) nested tug-of-war approach, where an individual's fitness, *w*, is given by the amount of resource it obtains. In a population of n_g groups competing over a resource of value *v*, an individual's fitness is determined by the fraction *p* of resource obtained by this individual's group (i.e. the group's productivity) and the fraction *q* of the group productivity obtained by the individual itself:

Equation 4.1

$$w_1 = vp_1q_1$$

$$w_2 = vp_2q_2$$

The resource itself can take any form, such as food or breeding opportunities, that can be converted into reproductive units. The within-group fraction *q* is determined by the ratio of the focal individual's selfish effort to others' in the group (Reeve et al. 1998), given that there is scramble competition over the resource the group has obtained (Cant 2012). The return on a given investment in selfish conflict varies between roles, where individuals in Role 2 may have a reduced competitive efficiency *b* relative to those in Role 1 ($0<b\leq1$). For example, if $b=0.5$, a given investment in competition by a Role 2 player is half as effective in determining the outcome of that competition relative to the same investment by a Role 1 player. This is analogous to individuals' power in the group (Beekman et al. 2003; Beekman and Ratnieks 2003).

An individual's neighbor-modulated fitness is determined by the effects on its direct fitness generated by the actions of others. In this model, therefore, it is a function of all group members' selfish investments, and we must consider (1) the focal individual's own selfish efforts, (2) those of others in the same role who do and do not share the same allele, and (3) those of others in the other role who do and do not share the same allele. We thus construct expressions for q_1 and q_2 as follows:

Equation 4.2

$$q_1 = {x_1}/{x_1 + (n_1 - 1)(r_{11}x_1 + (1 - r_{11})x_1{}^*) + n_2 b(r_{12}x_2 + (1 - r_{12})x_2{}^*)}$$

$$q_2 = {bx_2}/{bx_2 + (n_2 - 1)b(r_{22}x_2 + (1 - r_{22})x_2{}^*) + n_1(r_{21}x_1 + (1 - r_{21})x_1{}^*)}$$

In other words, the fraction of the group productivity that a focal individual receives, i.e. its share of reproduction relative to others in its group, is determined by the ratio of its selfish effort to the sum of the selfish efforts of all individuals in its group. For individuals in Role 2, selfish effort x_2 is modulated by the competitive efficiency factor b.

The fraction of the total resource that a group obtains, i.e. its productivity p, depends on its members' investment in cooperation, for example foraging effort by workers. The combined effort of all group members may be greater by a factor k than the sum of individual efforts, and thus the total cooperative investments, c, by groups with a focal mutant in Role 1, focal mutant in Role 2, and no mutant individuals are respectively:

Equation 4.3

$$c_1 = k((1 - x_1) + (n_1 - 1)(r_{11}(1 - x_1) + (1 - r_{11})(1 - x_1{}^*)) + n_2(r_{12}(1 - x_2) + (1 - r_{12})(1 - x_2{}^*))$$

$$c_2 = k((1 - x_2) + (n_2 - 1)(r_{22}(1 - x_2) + (1 - r_{22})(1 - x_2{}^*)) + n_1(r_{21}(1 - x_1) + (1 - r_{21})(1 - x_1{}^*))$$

$$c^* = k(n_1(1 - x_1{}^*) + n_2(1 - x_2{}^*))$$

Given that groups are engaged in competition over productivity ("production competition", *sensu* Cant 2012), the fraction *p* of the total resource that each group obtains is the ratio of its total cooperative effort to the efforts of n_g-1 other groups (Reeve and Hölldobler 2007). We assume that the intensity of within-group competition is the same as the intensity of between-group competition (see appendix) and that there is a zero probability of individuals in another group possessing by common descent the mutant allele present in individuals in the focal group. The fractions of resource obtained by groups with a focal mutant in Role 1 and in Role 2 respectively are therefore:

Equation 4.4

$$p_1 = {c_1}\Big/{c_1 + (n_g - 1)c^*}$$

$$p_2 = {c_2}\Big/{c_2 + (n_g - 1)c^*}$$

We then substitute the expressions for q_1, q_2, p_1 and p_2 into w_1 and w_2. The probability that an individual is in each role is given by the proportion of group members in that role. An individual's expected fitness w across both roles is therefore:

Equation 4.5

$$w = \frac{n_1}{n_1 + n_2} w_1 + \frac{n_2}{n_1 + n_2} w_2$$

Analyzing the model

In order to obtain the ESS pair x_1* and x_2* that maximizes an individual's fitness, we find the partial derivatives $\frac{\partial w}{\partial x_1}$ and $\frac{\partial w}{\partial x_2}$. At equilibrium, the partial derivatives are equal to zero, x_1 is equal to x_1*, and x_2 is equal to x_2*. We simultaneously solve this pair of equations for the evolutionarily stable pair of solutions x_1* and x_2*, and verify that these values are fitness maxima by checking that $\frac{\partial^2 w}{\partial {x_1}^2}$ and $\frac{\partial^2 w}{\partial {x_2}^2}$ are negative. We also identified stable boundary solutions (x*=0 or 1): we set one of x_1* and x_2* equal to one of the boundary values and solved for the stable solution in the other variable, by setting the partial derivative of fitness with respect to the non-boundary variable to zero. We then checked for stability by determining whether the first derivative of the boundary solution was negative (if x=0) or positive (if x=1) while the second derivative with respect to the other variable was negative at the solution.

We used Mathematica 8.0 (Wolfram Research) to analyze the model, and were unable to obtain analytical solutions. For simplicity, unless otherwise stated, we restrict the numerical results below to those appropriate to monogynous hymenopteran societies, which are the focus of this model. We consider a single individual in Role 1 (n_1=1), with r_{12}=r_{21}=0.5: that is, individuals in Role 2 are worker daughters of the single queen in Role 1. Additionally, $r_{22} = \frac{1}{4}+\frac{1}{2m}$, where m is the queen's mating frequency, and thus $0.25 \leq r_{22} \leq 0.75$ (in the appendix, we present results for $0 \leq r_{22} \leq 1$).

RESULTS

Overview

When b=1 and r_{12}=r_{21}=r_{22} (or r_{12}=r_{21} and n_2=1), the game is symmetrical, and yields the same numerical results as Reeve and Hölldobler's (2007) symmetrical analytical model. When the game is asymmetrical, an individual in Role 2 generally contributes more to group productivity (i.e., invests more in cooperation) but receives a smaller fraction of the benefits of this productivity (i.e., a smaller share of reproduction) than does an individual in Role 1, except when relatedness between members of Role 1 (r_{22}) is low.

Number of competing groups (n_g)

Individuals in both Role 1 and Role 2 increase their cooperative efforts ($1-x_1^*$ and $1-x_2^*$ respectively) as the number of competing groups (n_g) increases, but for low n_g only (Figure 4.1a-b). Similarly, the Role 1 player receives a larger share of reproduction (q_1) for increasing but small n_g, while a Role 2 player's share (q_2) is insensitive to the number of competing groups (Figure 4.1c-d). Given that the number of competing groups has an increasingly small effect on individuals' cooperative efforts and reproductive shares, for a range of values of n_2, b and r_{22} (Figure 4.1), in the following results we fix n_g=10.

Number of individuals in Role 2 (n_2)

When there are many individuals in Role 2 (high n_2), they are highly related to each other and competitively inefficient relative to the Role 1 individual (b<1), the Role 1 player invests zero in cooperative group productivity, and each Role 2 player invests almost everything. In contrast, when Role 2 players are not highly related (low r_{22}), the Role 1 player invests much and each Role 2 player invests little in cooperation when n_2 is high: thus, the effect of changing n_2 is highly sensitive to r_{22} (Figure 4.2a-b). Additionally, the effect of increasing n_2 is greatest when n_2 is already low (i.e. decelerating effect), and when b is low (Figure 4.3a-b).

Both the Role 1 and Role 2 players receive a smaller fraction of resources when there are more individuals in Role 2 (Figures 4.2c-d, 4.3c-d), particularly when b is higher.

Relatedness asymmetry (r_{22})

When the Role 1 and Role 2 individuals are symmetrically related to each other (i.e., the probability of an allele being carried by an individual in one role, given that it is carried by an individual in the other role, is the same, regardless of the role) by $r_{12}=r_{21}=0.5$ (e.g. mother and daughters), higher relatedness among Role 2 individuals (r_{22}) results in higher cooperation by each individual in Role 2, but lower cooperation by the Role 1 player (Figures 4.2a-b, 4.4a-b). This effect is particularly strong when there are more individuals in Role 1 (high n_2) and they are more competitively equal to the individual in Role 1 (high b): indeed, in the latter case, the Role 1 player invests zero in cooperation. However, when relatedness among Role 2 individuals is low and either n_2 or b is high, the Role 1 player invests a lot and the Role 2 player invests very little in cooperation.

In contrast, the fraction of group resources obtained by each party is relatively insensitive to r_{22} (Figures 4.2c-d, 4.4c-d).

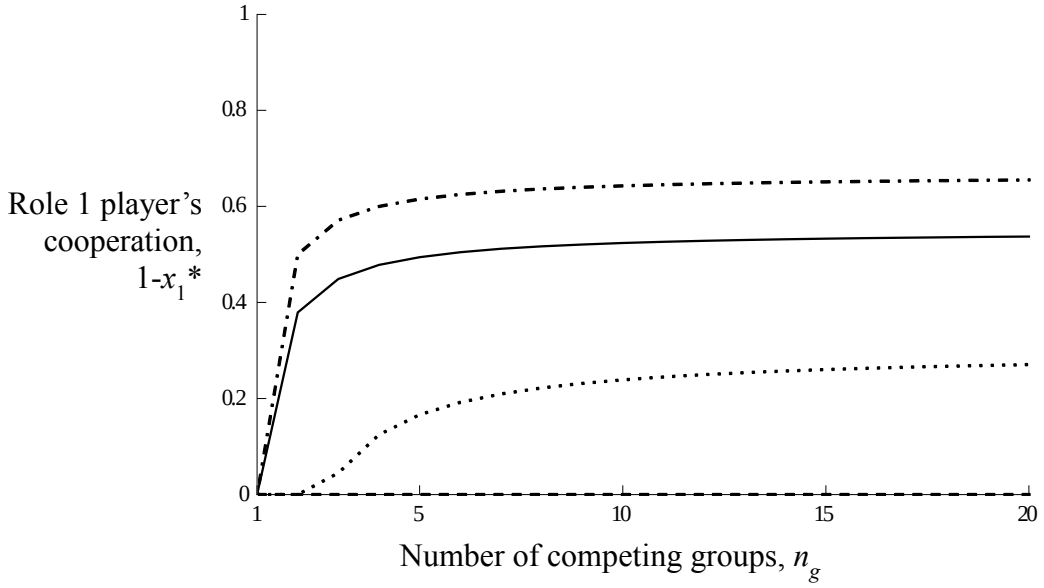
Competitive asymmetry (b)

When individuals in each role are more evenly competitively matched (b approaches 1), the Role 1 player invests more in cooperation, and each Role 2 player invests less (Figures 4.3a-b, 4.4a-b). The effect of b is greatest when Role 2 players are not highly related to each other (r_{22} is lower) and there are more Role 2 players in the group (n_2 is higher).

As b increases, the Role 1 player obtains a smaller share of reproduction and each Role 2 player obtains a larger share (Figures 4.3c-d, 4.4c-d). The Role 1 player's share is more sensitive to b

than is a Role 2 player's, and is most sensitive to *b* when there are more individuals in Role 2 and they are less related to each other.

(a)



(b)

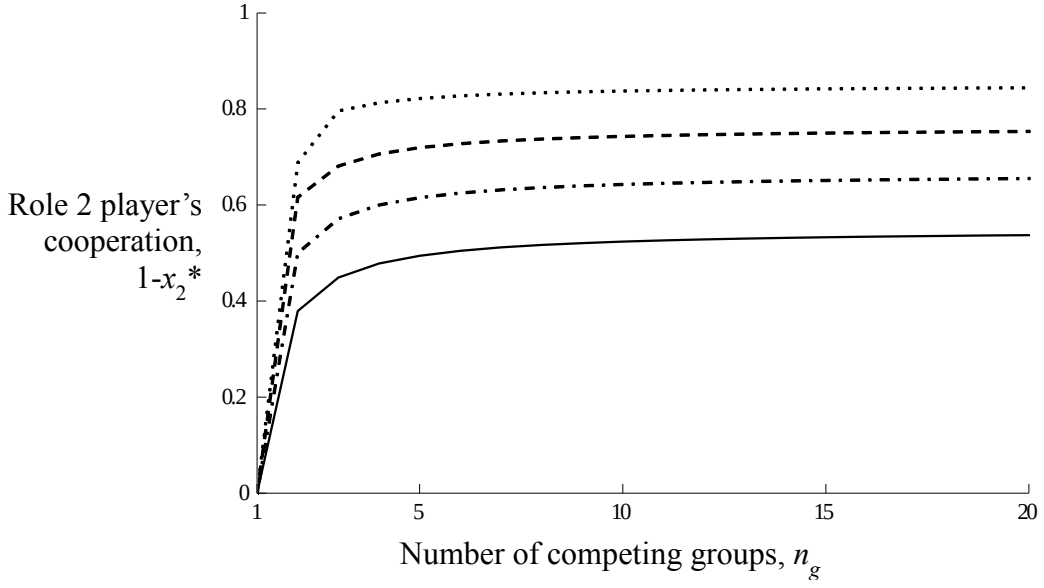
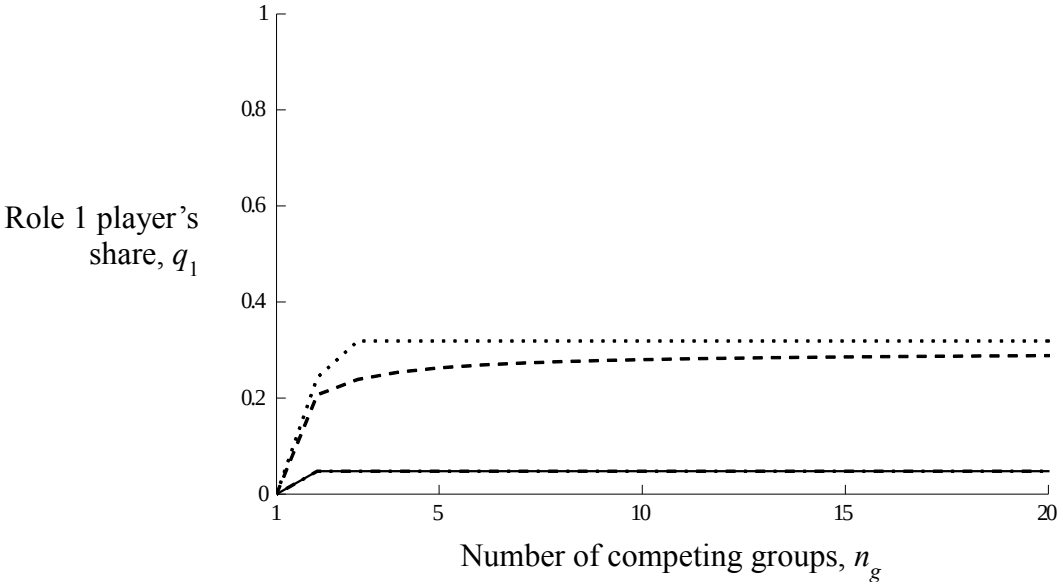


Figure 4.1. The effect of the number of competing groups, n_g, on: (a) the Role 1 player's contribution to group productivity, and (b) a Role 2 player's contribution to group productivity. Each group has a single individual in Role 1 (n_1=1), who is related to individuals in Role 2 by 0.5, and vice versa (r_{12}=r_{21}=0.5). Solid lines: n_2=10, b=1, r_{22}=0.5; dot-dashed lines: n_2=1, b=1, r_{22}=0.5; dotted lines: n_2=10, b=0.1, r_{22}= 0.5; dashed lines: n_2=10, b=1, r_{22}=0.75.

(c)



(d)

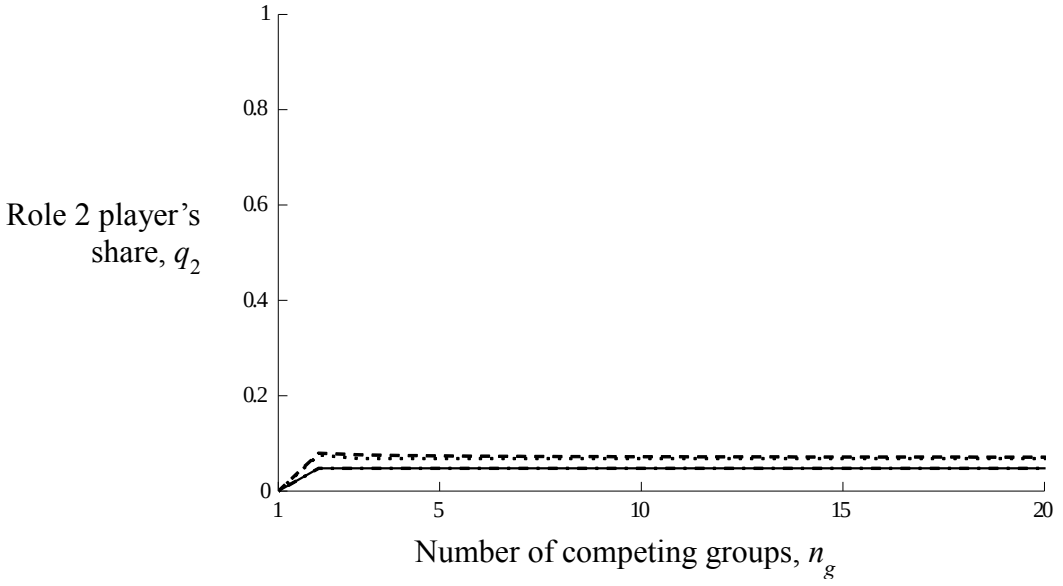
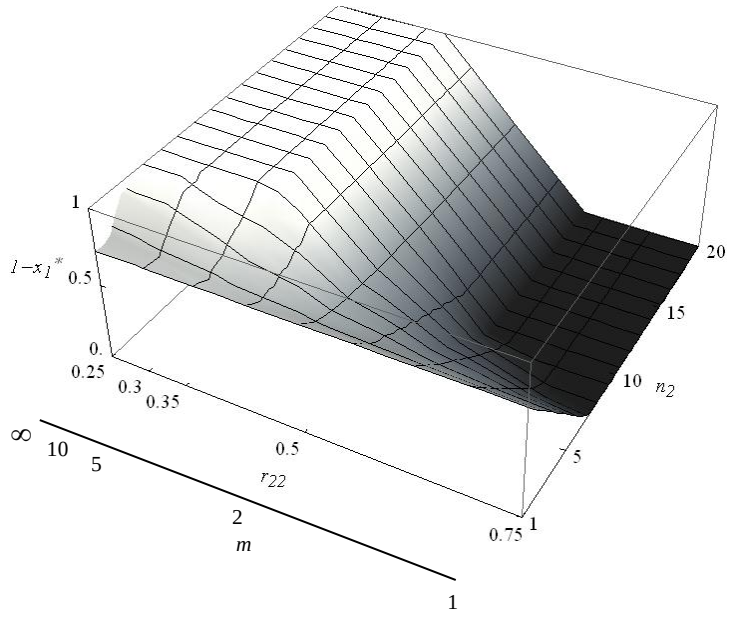


Figure 4.1 continued. The effect of the number of competing groups, n_g, on: (c) the Role 1 player's share of reproduction, and (d) a Role 2 player's share of reproduction. Each group has a single individual in Role 1 (n_1=1), who is related to individuals in Role 2 by 0.5, and vice versa (r_{12}=r_{21}=0.5). Solid lines: n_2=10, b=1, r_{22}=0.5; dot-dashed lines: n_2=1, b=1, r_{22}=0.5; dotted lines: n_2=10, b=0.1, r_{22}= 0.5; dashed lines: n_2=10, b=1, r_{22}=0.75.

(a)



(b)

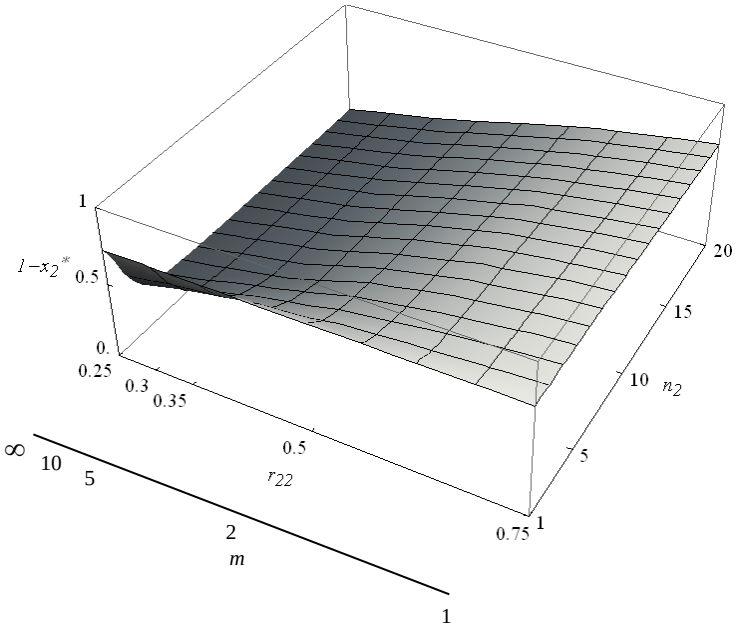
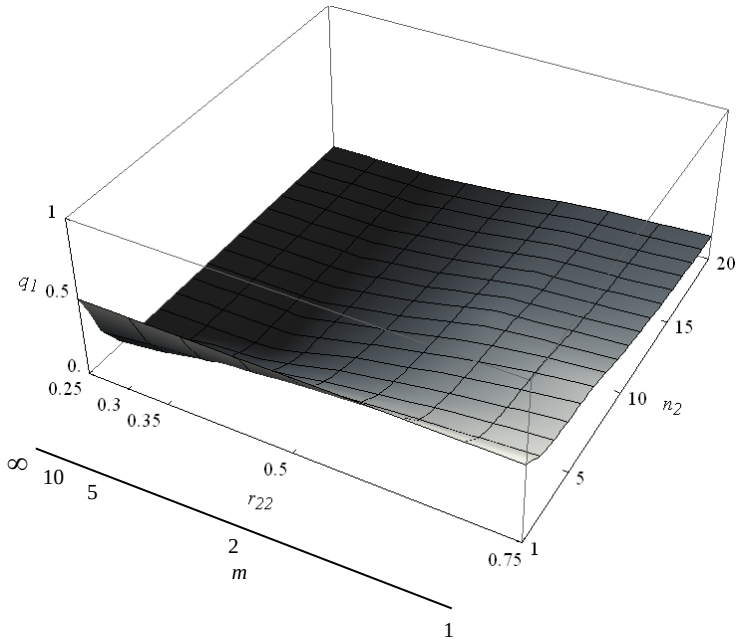


Figure 4.2. The effect of the number of individuals in Role 2, n_2, and their relatedness to each other, r_{22}, on: (a) the Role 1 player's contribution to group productivity, and (b) a Role 2 player's contribution to group productivity. Ten groups are competing over the resource (n_g=10). Each group has a single Role 1 player (n_1=1); individuals in one role are symmetrically related to those in the other role by 0.5 (r_{12}=r_{21}=0.5), and there is no asymmetry in competitive efficiency (b=1). The black bar shows how, in Hymenoptera, the Role 1 player's (i.e., the queen's) mating frequency, m, corresponds to relatedness among Role 2 players (i.e., the workers), r_{22}.

(c)



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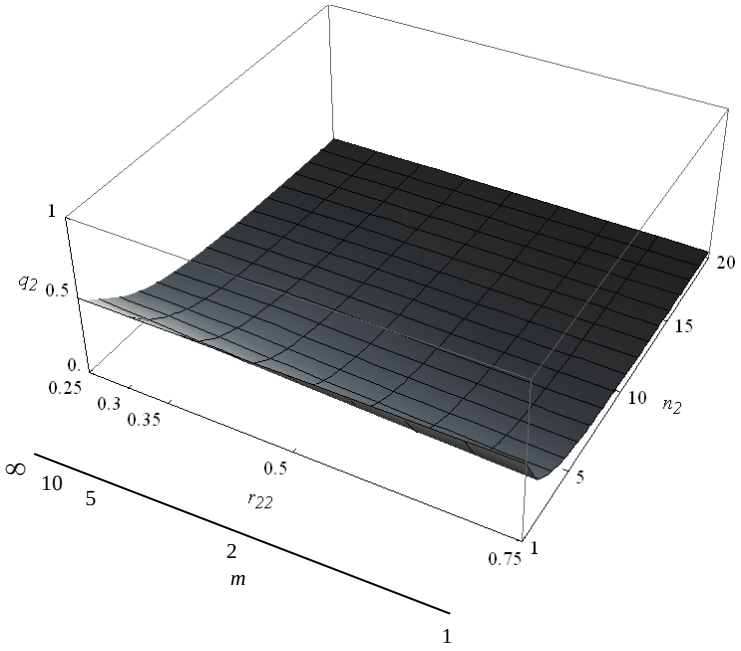
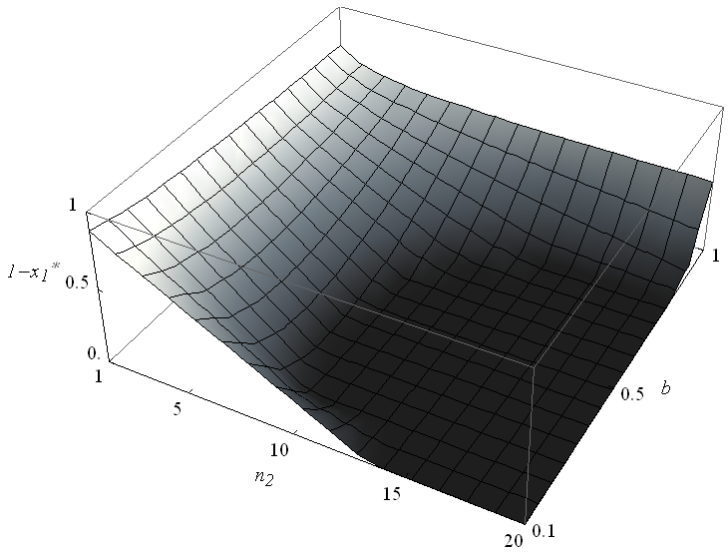


Figure 4.2. The effect of the number of individuals in Role 2, n_2, and their relatedness to each other, r_{22}, on: (c) the Role 1 player's share of reproduction, and (d) a Role 2 player's share of reproduction. Ten groups are competing over the resource (n_g=10). Each group has a single Role 1 player (n_1=1); individuals in one role are symmetrically related to those in the other role by 0.5 (r_{12}=r_{21}=0.5), and there is no asymmetry in competitive efficiency (b=1). The black bar shows how, in Hymenoptera, the Role 1 player's (i.e., the queen's) mating frequency, m, corresponds to relatedness among Role 2 players (i.e., the workers), r_{22}.

(a)



(b)

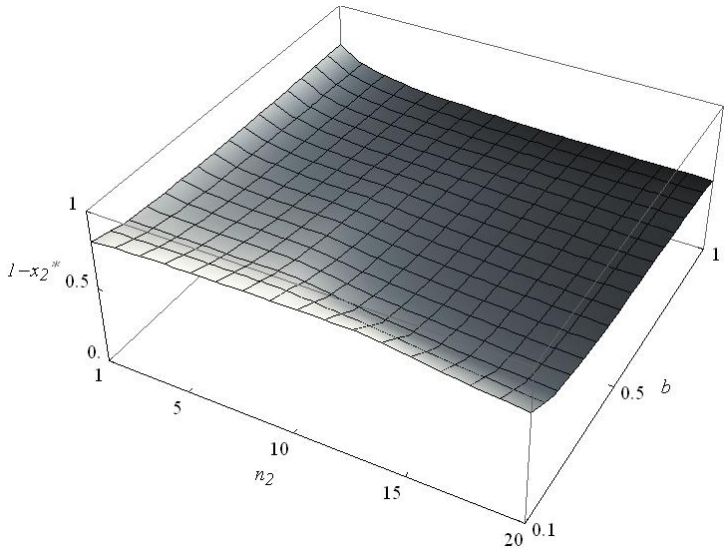
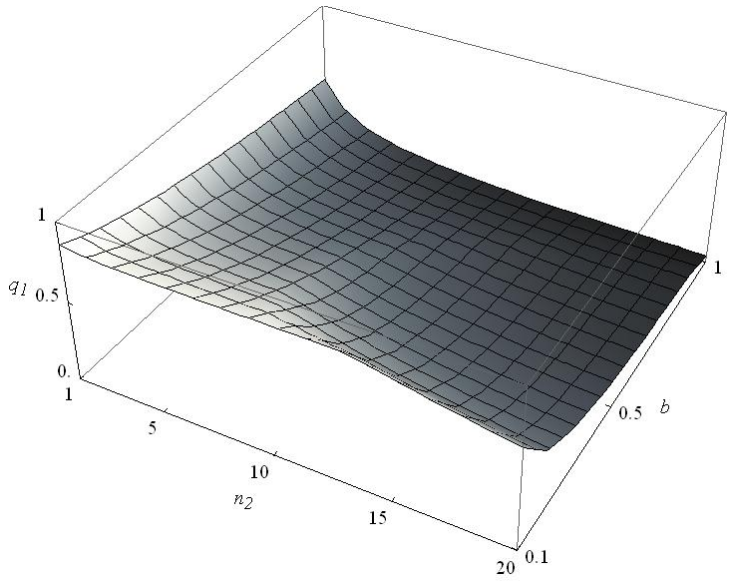


Figure 4.3. The effect of the number of individuals in Role 2, n_2, and their competitive efficiency relative to individuals in Role 1, b, on: (a) the Role 1 player's contribution to group productivity, and(b) a Role 2 player's contribution to group productivity. Ten groups are competing over the resource (n_g=10). Each group has a single individual in Role 1 (n_1=1); all group members are related to each other by 0.5 (r_{12}=r_{21}=r_{22}=0.5); that is, relatedness is symmetrical, and the only asymmetries are in n_2 and b.

(c)



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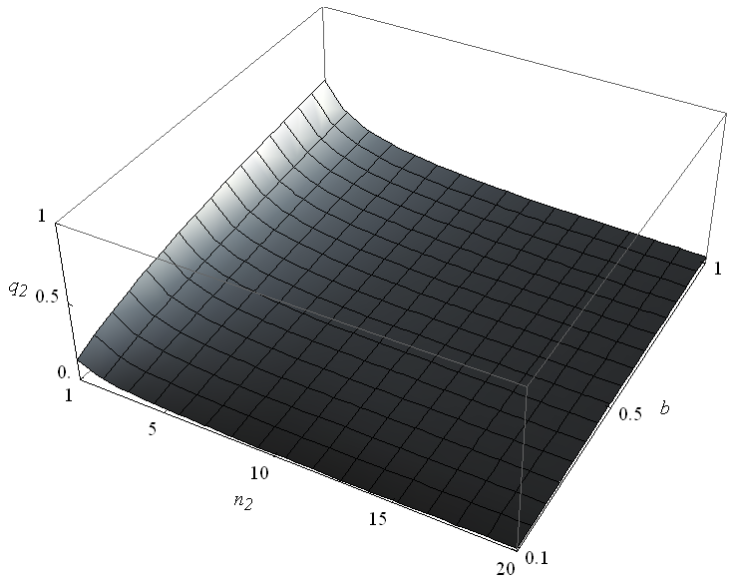


Figure 4.3. The effect of the number of individuals in Role 2, n_2, and their competitive efficiency relative to individuals in Role 1, b, on: (c) the Role 1 player's share of reproduction, and (d) a Role 2 player's share of reproduction. Ten groups are competing over the resource (n_g=10). Each group has a single individual in Role 1 (n_1=1); all group members are related to each other by 0.5 (r_{12}=r_{21}=r_{22}=0.5); that is, relatedness is symmetrical, and the only asymmetries are in n_2 and b.

(a)

(b)

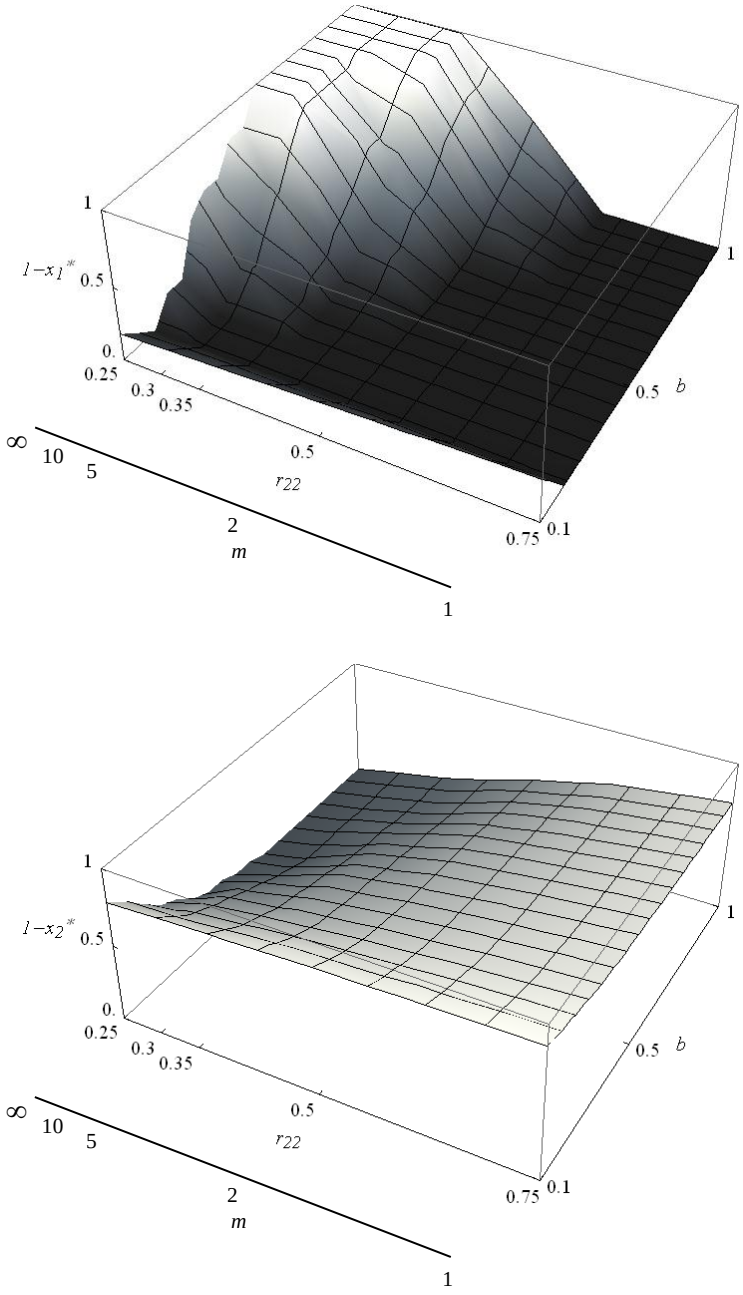
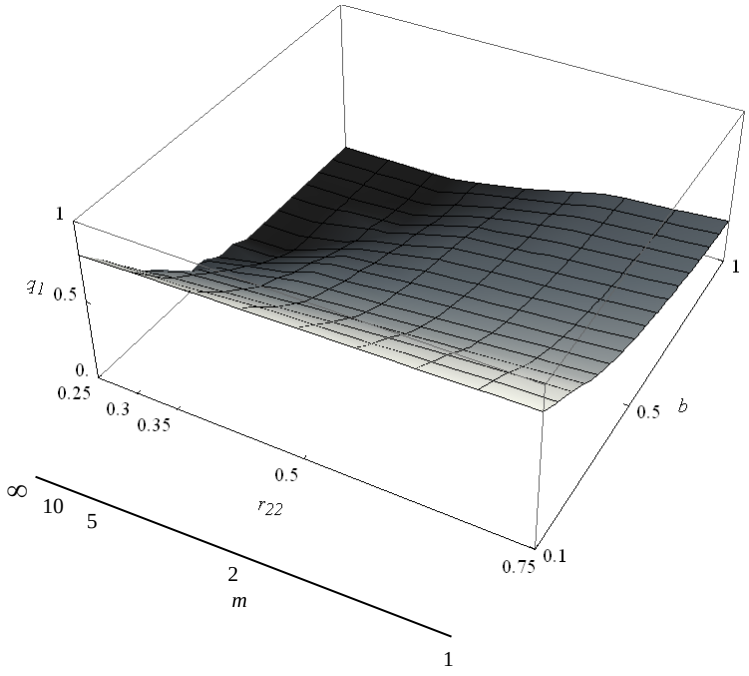


Figure 4.4. The effect of Role 2 players' competitive efficiency, *b*, and their relatedness to each other, r_{22}, on: (a) the Role 1 player's contribution to group productivity, and (b) a Role 2 player's contribution to group productivity. Ten groups are competing over the resource (n_g=10); each group consists of a single individual in Role 1 (n_1=1) and ten in Role 2 (n_2=10). Individuals in one role are symmetrically related to those in the other role by 0.5 (r_{12}=r_{21}=0.5).The black bar shows how, in Hymenoptera, the Role 1 player's (i.e., the queen's) mating frequency, *m*, corresponds to relatedness among Role 2 players (i.e., the workers), r_{22}.

(c)



(d)

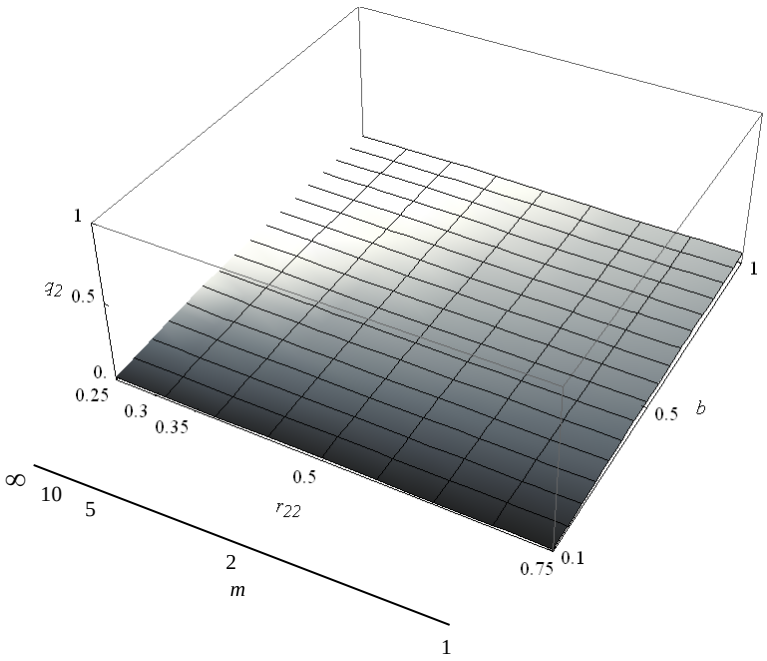


Figure 4.4. The effect of Role 2 players' competitive efficiency, *b*, and their relatedness to each other, r_{22}, on: (c) the Role 1 player's share of reproduction, and (d) a Role 2 player's share of reproduction. Ten groups are competing over the resource (n_g=10); each group consists of a single individual in Role 1 (n_1=1) and ten in Role 2 (n_2=10). Individuals in one role are symmetrically related to those in the other role by 0.5 (r_{12}=r_{21}=0.5).The black bar shows how, in

Hymenoptera, the Role 1 player's (i.e., the queen's) mating frequency, m, corresponds to relatedness among Role 2 players (i.e., the workers), r_{22}.

DISCUSSION

We found that when an individual's behavior is allowed to differ depending on the role it adopts within a group (i.e. potential within-group asymmetry), intergroup competition results in increased within-group cooperation, as for symmetrical groups with a single behavioral role (Reeve and Hölldobler 2007). Two important points emerge from the asymmetric model presented here. Firstly, not all individuals cooperate: for the range of parameters used here, the individual in Role 1 generally invests less in cooperation than does an individual in Role 2, and sometimes does not cooperate at all. As in the symmetrical model, few competing groups in the population need be present in order to favor within-group cooperation, and the presence of additional groups does not affect the level of cooperation. Secondly, not all individuals reap the benefits of this cooperation: in most cases, the Role 1 player gains a larger share of the group's productivity than does a Role 2 player, and the number of competing groups has little effect on this. Given that there is wide variation in the distribution among group members of cooperation (for example, based on dominance: Cant and Field 2005) and reproduction (skew: Sherman et al. 1995; Lacey and Sherman 2005), this model provides a more accurate picture of real social groups than does a symmetric game.

As this study was motivated by expanding the intergroup competition model to hymenopteran groups (Reeve and Hölldobler 2007), we used numerical parameter values appropriate for haplodiploid mother-daughter societies, with the mother in Role 1 and daughters in Role 2. Thus, the Role 1 player may be considered the queen, and the Role 2 players the workers (these terms used interchangeably hereafter). Unlike many other models of social evolution, here we do not

assume that workers are coerced by policing (Frank 2003; Wenseleers et al. 2004) or that they are somatic extensions of the queen (Nowak et al. 2010); that is, in this model, workers are free to make their decision in the context of asymmetry in relatedness, worker number, and competitive efficiency, and this decision coevolves with the queen's. Furthermore, note that although the optimal behavior of a Role 1 player is typically associated with within-group dominance, and that of a Role 2 player with subordinance, these roles are not intrinsically "dominant" and "subordinate", especially if individuals in each role have the same competitive efficiency (b=1). The predictions emerged simply by assigning realistic values to the relatedness and group size parameters; these values may easily be substituted for others in order to make the model more general (see appendix). Below, we discuss the effects of changing the values of the parameters in the model.

Effects of within-group asymmetries on cooperation and skew

When there are more individuals in Role 2 (higher n_2), both the workers (Role 2) and the queen (Role 1) invest less in cooperation, as predicted by the symmetrical model (Reeve and Hölldobler 2007), and obtain smaller shares of the resource. This is because individuals can parasitize others' cooperative investments in group productivity, which are then divided among more individuals. Although it is already known that per capita group productivity decreases as group size increases (Reeve and Hölldobler 2007 and references therein), the novel prediction here is that both a queen and workers' investments in productivity decrease as the number of workers increases. A simple test of this prediction would be an intraspecific comparison of queens' contributions to group productivity in differently sized colonies of a primitively eusocial

taxon, such as *Polistes* wasps, noting that queens may contribute to group productivity in different ways than do workers (O'Donnell 1998).

In hymenopteran societies with a single queen, the probabilities that an allele in a given individual is also found in another individual, due to common descent, are $r_{12}=r_{21}=0.5$ between the queen and a worker, and vice versa. Between two workers, $r_{22} = \frac{1}{4}+\frac{1}{2m}$, where m is the queen's mating frequency and $0.25<r_{22}<0.75$. Using these numerical values, the model predicts that the queen (Role 1) cooperates less and workers (Role 2) cooperate more when the queen has a lower mating frequency and thus worker-worker relatedness is higher (Boomsma 2007; Boomsma 2009). As in the symmetrical model, when r_{22} decreases, workers benefit less from investing in within-group competition, particularly when there are more workers (high n_2): this means that the group obtains less resource, and thus the queen, whose relatedness to the workers is fixed, benefits by investing more in cooperative group productivity. One would therefore predict more potential conflict among workers in colonies with a multiply mated queen. Note, however, that multiple mating selects for worker policing (Ratnieks 1988), but that the model here allows individuals to make optimal decisions in the absence of any coercion or policing. Thus, conflict reduction mechanisms are likely to prevent the high potential conflict predicted at low worker relatedness from becoming actual conflict (Ratnieks and Reeve 1992).

A further parameter of asymmetry absent from the symmetric game is b, the competitive efficiency of an individual in Role 2 relative to an individual in Role 1. In many societies, individuals differ in their "power" to affect the outcome of a conflict (Beekman et al. 2003), and thus it is important to take this parameter into account. Here, we combine the framework of a

single-group, asymmetric 2-player tug-of-war skew model (Reeve et al. 1998) with the intergroup, symmetric *n*-player nested tug-of-war model (Reeve and Hölldobler 2007). Thus, we generate the prediction that when *b* is lower, an individual in Role 1 (queen) cooperates less but an individual in Role 2 (worker) cooperates more. In this case, workers get a low return on any investment in within-group competition, which (1) favors greater investment in cooperation, and (2) results in each worker obtaining a smaller share of the group's resource (i.e. reproductive opportunities), as in the 2-player model (Reeve et al. 1998).

Although this prediction is testable, attempts to quantify individuals' relative competitive abilities in insect societies have had mixed success. For example, there is conflicting evidence in *Polistes* wasps for predictors of success in agonistic interactions, with body size, age, facial markings and order of arrival at the nest among the factors implicated in dominance (Hughes and Strassmann 1988; Seppä et al. 2002; Tibbetts and Dale 2004; Cervo et al. 2008; Zanette and Field 2009; Green and Field 2011). However, we might expect workers who are morphologically more distinct from the queen to have a lower relative competitive efficiency, since their specialization may make them less able to participate in competition over shares of group productivity (Bourke 1999). According to the maternal manipulation hypothesis (Alexander 1974), larval feeding can affect queen-worker morphological divergence (Wheeler 1986), for example in sweat bees, *Megalopta genalis* (Kapheim et al. 2011); this could potentially be a mechanism to reduce worker competitive efficiency (Beekman and Ratnieks 2003). Such a mechanism may be more likely to be favored when there are more workers, given that workers in larger colonies invest less in cooperation. Indeed, there is more elaborate worker specialization and complex division of labor in larger colonies (Bourke 1999).

Extending the model

In order to focus our numerical analyses, we did not analyze all possible parameter values in the model. Two assumptions in particular, that there is only one individual in Role 1 (queen) and that individuals in a given group are unrelated to members of other groups, could be relaxed and explored using the same model framework.

The assumption that each group contains a single queen (n_1=1) with a varying number of worker offspring (n_2) is true for many insect societies, such as honeybees and vespine wasps (Wilson 1971), but many other insect societies exhibit variation in queen number (Keller 1993; Bourke and Heinze 1994). In order to incorporate multiple queens into the model, one would set n_1>1, and assign a value to r_{11} (e.g. 0.75, if queens are full sisters). The latter value determines the other relatednesses: for example, if all queens produce worker offspring, r_{12} would be a queen's average relatedness to any given worker. Intuitively, one might predict individuals in Role 1 (queens) to invest less in cooperation when n_1 increases and when r_{11} decreases; indeed, many of the most complex cooperative societies (that is, those with highly specialized worker castes, for example in honeybee, army ant, and leafcutter ant colonies) have single queens (Bourke 1999).

When constructing the model, we assumed complete dispersal of new reproductives, such that group members are unrelated to individuals in other groups. This allowed us to focus on the effects of within-group asymmetries in the most basic scenario of competition with unrelated groups. However, there is evidence for female philopatry in some hymenopteran societies (Johnstone et al. 2012): thus, if a focal individual carries an allele for the mutant strategy *x*, there

is a non-zero probability that individuals in other groups also carry the allele for *x*. This probability would depend on how closely the queens are related to each other (e.g. queens in neighboring groups are full or half-sisters), and, in constructing the model, would be incorporated into the expression for *p*, the ratio of groups' cooperative efforts. One might expect both a queen's (Role 1) and worker's (Role 2) within-group cooperation to decrease, all else being equal, if they are more related to individuals in competing groups, as in a symmetrical game (West et al. 2002; Reeve and Hölldobler 2007).

Summary

The tug-of-war model presented here generates several testable predictions about the degree of within-group cooperation in asymmetrical groups. This model provides a more realistic view of intra-group behavior than (a) a symmetrical model, since group members are undoubtedly not all the same, and (b) a single-group model, since groups rarely exist in isolation, but instead are embedded in a population of other groups. By incorporating within-group asymmetries, this model is able to make predictions, for example about the equitability of within-group resource sharing, that a symmetrical model is unable to make. The model's predictions can be applied not just to hymenopteran insects, but to any other social organisms, from bacteria (Griffin et al. 2004; Brockhurst et al. 2007) and slime molds (Strassmann et al. 2000) to cooperatively breeding vertebrates (Solomon and French 1997; Koenig and Dickinson 2004; Hager and Jones 2009). This paves the way for empirical tests in diverse taxa, ultimately shedding light on unifying evolutionary principles governing the balance between cooperation and competition.

APPENDIX

1. Intensity of competition

When the intensity of within-group competition, *y*, is equal to 1, an individual that invests *t* times as much in selfishness relative to others' investments receives a fraction *t* times greater of the resource. However, when the intensity of within-group competition is low (y<1), additional investment in selfishness results in a smaller increase in the fraction of resource; in contrast, a very high *y* (>1) describes an intense winner-takes-all competition. Incorporating *y*, the within-group shares of a focal mutant individual in Role 1 and Role 2 respectively are:

Equation S4.1

$$q_1 = {x_1}^y \Big/ {x_1}^y + (n_1 - 1)(r_{11}{x_1}^y + (1 - r_{11}){x_1}^{*y}) + n_2 b(r_{12}{x_2}^y + (1 - r_{12}){x_2}^{*y})$$

$$q_2 = b{x_2}^y \Big/ b{x_2}^y + (n_2 - 1)b(r_{22}{x_2}^y + (1 - r_{22}){x_2}^{*y}) + n_1(r_{21}{x_1}^y + (1 - r_{21}){x_1}^{*y})$$

Similarly, the exponent *z* describes the intensity of between-group competition, i.e. the extent to which a group's additional investment in *c* increases the fraction of resource *p* that it obtains. These fractions acquired by groups with a focal mutant individual in Role 1 and Role 2 respectively are:

Equation S4.2

$$p_1 = {c_1}^z \Big/ {c_1}^z + (n_g - 1)c^{*z}$$

$$p_2 = {c_2}^z \Big/ {c_2}^z + (n_g - 1)c^{*z}$$

We substitute these expressions for q_1, q_2, p_1 and p_2 into the fitness function w and obtain numerical solutions, as before.

When the intensity of between-group competition z increases relative to the intensity of within-group competition y, both parties increase their investments in cooperation (results not shown). This corroborates others' findings that cooperation decreases with local competition and increases with global competition (West et al. 2006; Reeve and Hölldobler 2007).

2. Full range of subordinate relatedness values

Below we present numerical results for the entire range of Role 2 – Role 2 relatedness values ($0 \leq r_{22} \leq 1$). As before, each group has a single individual in Role 1 ($n_1=1$); individuals in Role 1 and Role 2 are symmetrically related to each other by 0.5 ($r_{12}=r_{21}=0.5$).

When r_{22} is low, a Role 2 player invests less in cooperation than does the Role 1 player (Figures S4.1a-b, S4.2a-b). The magnitude of r_{22} changes the effect on within-group cooperation of increasing the number of Role 2 players: when r_{22} is high, the Role 1 player's cooperation

decreases and a Role 2 player's increases when there are more individuals playing Role 2 (high n_2), but the opposite is true for low r_{22}.

When r_{22} is higher, the Role 1 player receives a larger share of reproduction, but each Role 2 player receives a smaller share; the size of a Role 2 player's share is less sensitive to r_{22} than is the Role 1 player's share (Figures S4.1c-d, S4.2c-d). This contrasts with the two-player asymmetric tug-of-war, where skew is independent of r. One might predict from the n-player model presented here that skew would be lower in colonies with a multiply mated queen in Role 1.

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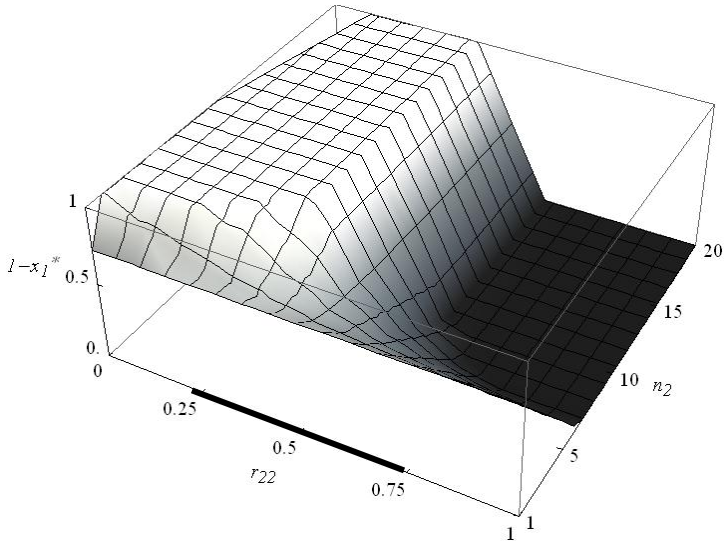
(a)



(b)

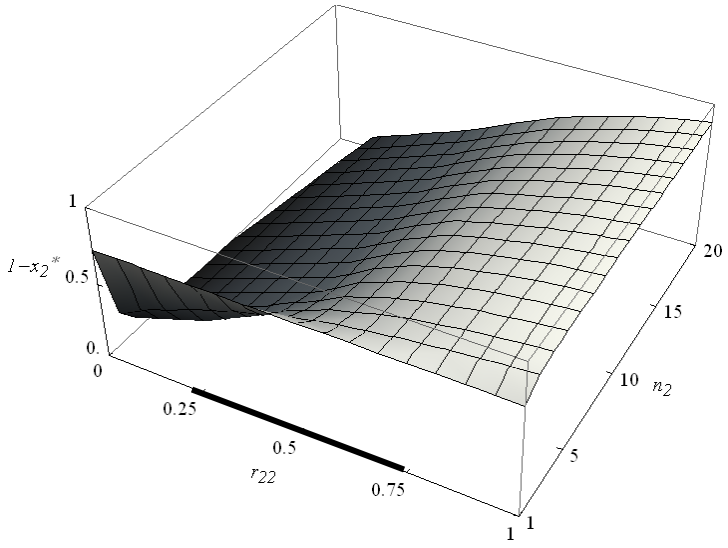
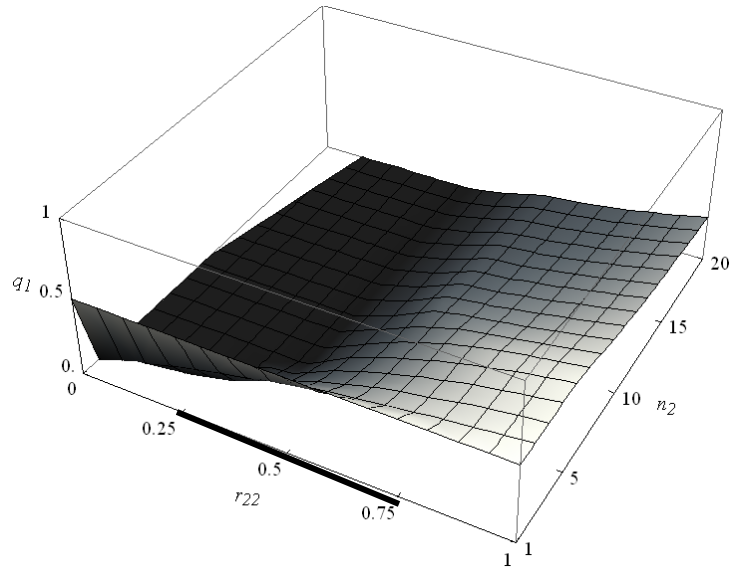


Figure S4.1. The effect of the number of individuals in Role 2, n_2, and their relatedness to each other, r_{22}, on: (a) the Role 1 player's contribution to group productivity, and (b) a Role 2 player's contribution to group productivity. Ten groups are competing over the resource (n_g=10). Each group has a single individual playing Role 1 (n_1=1); individuals in one role are symmetrically related to those in the other role by 0.5 (r_{12}=r_{21}=0.5), and there is no asymmetry in competitive efficiency (b=1). The black bar shows the range of r_{22} values in hymenopteran groups, where the queen is in Role 1 and workers are in Role 2 (as presented in main text, Figure 4.2).

(c)



(d)

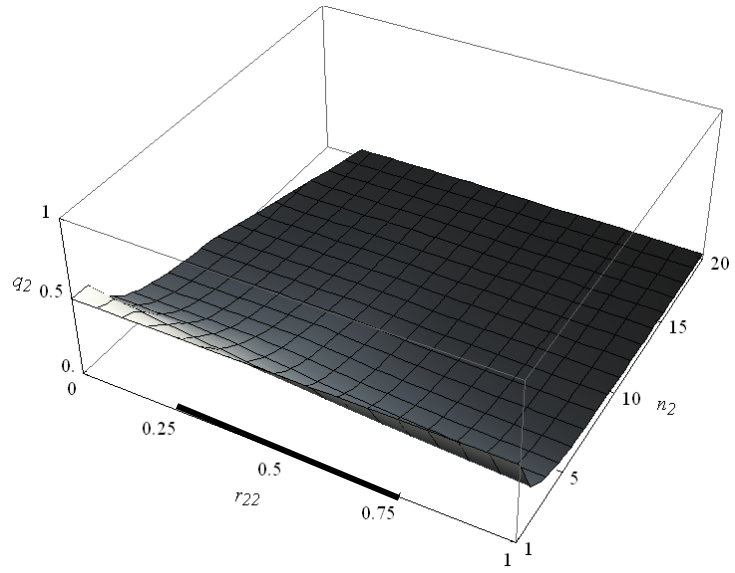
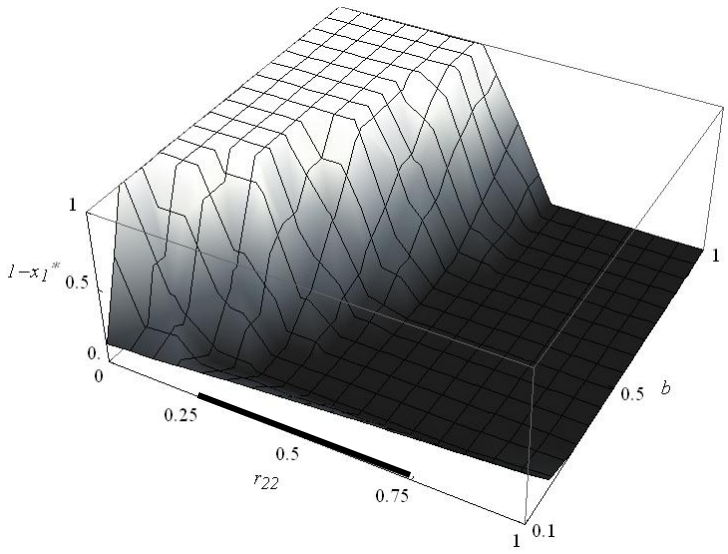


Figure S4.1 continued. The effect of the number of individuals in Role 2, n_2, and their relatedness to each other, r_{22}, on: (c) the Role 1 player's share of reproduction, and (d) a Role 2 player's share of reproduction. Ten groups are competing over the resource (n_g=10). Each group has a single individual playing Role 1 (n_1=1); individuals in one role are symmetrically related to those in the other role by 0.5 (r_{12}=r_{21}=0.5), and there is no asymmetry in competitive efficiency (b=1). The black bar shows the range of r_{22} values in hymenopteran groups, where the queen is in Role 1 and workers are in Role 2 (as presented in main text, Figure 4.2).

(a)



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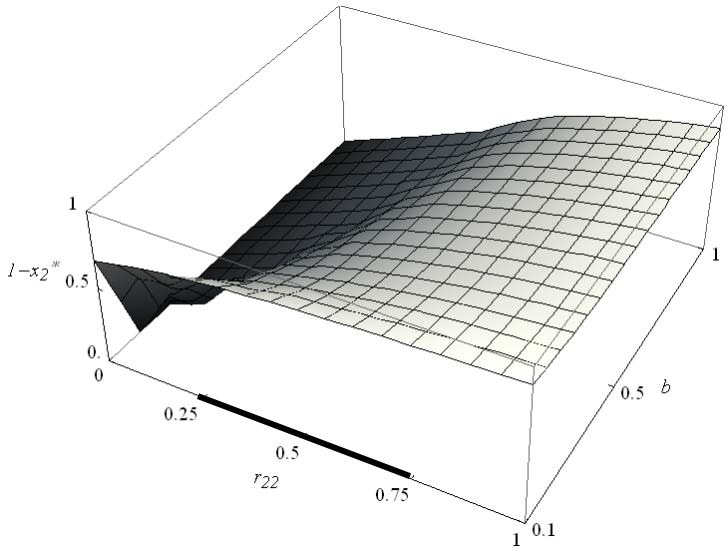
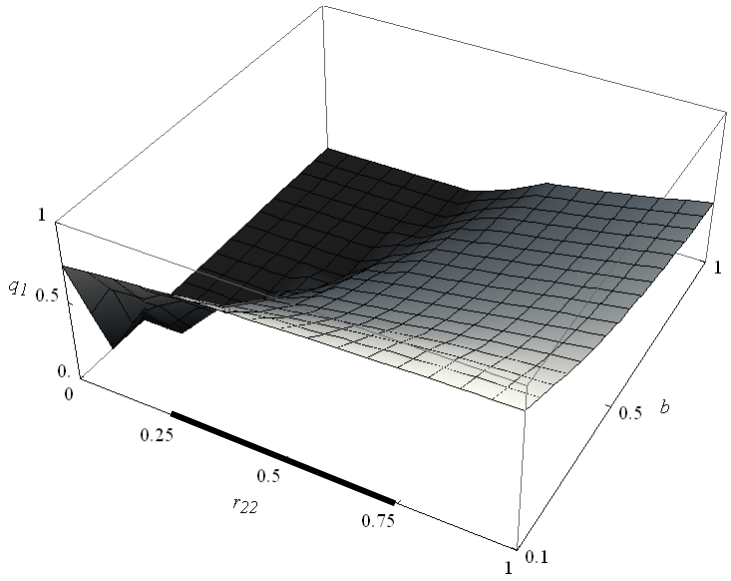


Figure S4.2. The effect of Role 2 players' competitive efficiency, b, and their relatedness to each other, r_{22}, on: (a) the Role 1 player's contribution to group productivity, and (b) a Role 2 player's contribution to group productivity. Ten groups are competing over the resource (n_g=10); each group has a single individual playing Role 1 (n_1=1) and ten playing Role 2 (n_2=10). Individuals in one role are symmetrically related to those in the other role by 0.5 (r_{12}=r_{21}=0.5). The black bar shows the range of r_{22} values in hymenopteran groups, where the queen is in Role 1 and workers are in Role 2 (as presented in main text, Figure 4.4).

(c)



(d)

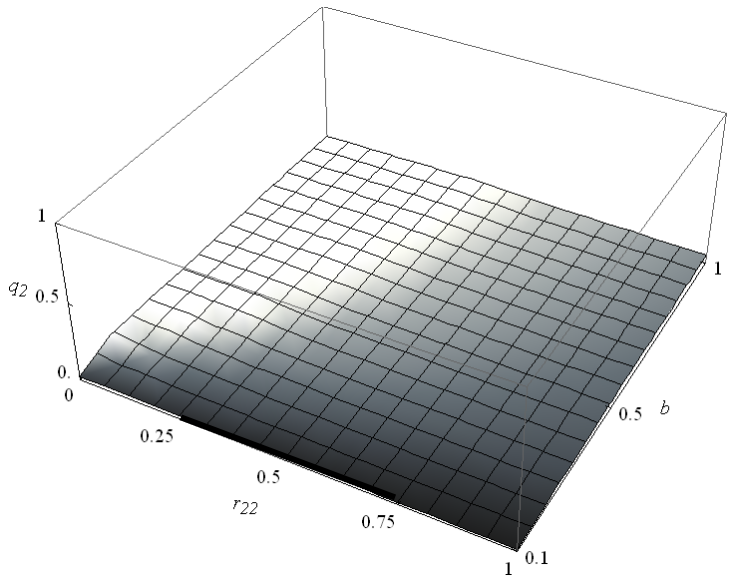


Figure S4.2 continued. The effect of Role 2 players' competitive efficiency, *b*, and their relatedness to each other, r_{22}, on: (c) the Role 1 player's share of reproduction, and (d) a Role 2 player's share of reproduction. Ten groups are competing over the resource (n_g=10); each group has a single individual playing Role 1 (n_1=1) and ten playing Role 2 (n_2=10). Individuals in one role are symmetrically related to those in the other role by 0.5 (r_{12}=r_{21}=0.5). The black bar shows the range of r_{22} values in hymenopteran groups, where the queen is in Role 1 and workers are in Role 2 (as presented in main text, Figure 4.4).

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CHAPTER 5

POTENTIAL CONFLICT OVER FORAGING IN A PRIMITIVELY EUSOCIAL WASP: INVESTIGATING AGGRESSION TOWARDS EXPERIMENTALLY REMOVED *POLISTES DOMINULUS* WORKERS

Jessica L. Barker and H. Kern Reeve

Evolutionary conflicts of interest between members of social groups lead to potential within-group conflict as well as cooperation. One form of potential conflict is over the effort that non-breeders invest in working or helping to raise the breeders' offspring. "Lazy" workers may impose a cost on other group members, which could select for group members to pay attention to how hard others are working. We experimentally removed workers in the primitively eusocial wasp *Polistes dominulus* during periods of high foraging activity, in order to determine whether nestmates responded to an individual worker's apparent lack of work. We found that focal removed workers who had access to food while removed received more aggression when they returned that those without food access, but the time they spent off the nest did not affect the aggression they received. These results are consistent with a hypothesized function of aggression as a means to obtain food forcibly from a returning forager. An alternative hypothesis, that aggression is used to punish "lazy" workers, is less strongly supported. We predict that punishment of lazy workers may occur when other group members suffer a net cost as a result of this laziness, and that workers will be more likely to be lazy when they have a higher probability of gaining direct fitness benefits.

INTRODUCTION

Social groups across the animal kingdom are not only characterized by cooperation among group members, but also by conflict (Emlen 1982; Frank 2003; Queller and Strassmann 2009; Cant 2012), even in highly cooperative eusocial insect groups (Bourke 1999; Ratnieks et al. 2006; Ratnieks and Wenseleers 2007; Strassmann and Queller 2007). Kin selection theory (Hamilton 1964) predicts that potential conflict will arise whenever group members have genetic conflicts of interest; such potential conflict may occur in several different scenarios. Conflict over caste determination (Bourke and Ratnieks 1999), sex ratios (Reuter and Keller 2001; Mehdiabadi et al. 2003) and worker male production (Hammond and Keller 2004) are specific to social Hymenoptera. However, other types of conflict occur in social groups of diverse taxa, such as competition over breeding opportunities; this may involve competing over access to mates, as in house mice *Mus domesticus* (Rusu and Krackow 2004) and meerkats *Suricata suricatta* (Clutton-Brock et al. 2006), or access to a breeding position or high rank in a dominance hierarchy, for example in many primates (Cowlishaw and Dunbar 1991) and social wasps (Strassmann 1981; Premnath, Sinha, and Gadagkar 1996; Cant et al. 2006). There may also be conflict over how much effort non-breeders invest (Komdeur and Heg 2005) in helping or working (here, we use these terms, and "helper" and "worker", interchangeably): this is the focus of the present experiment.

Conflict over the extent to which workers work can arise for two non-mutually exclusive kin-selected (Hamilton 1964) reasons. Firstly, the benefit of helping may vary, for example according to the helper's relatedness to the breeder. There is some evidence that less related

helpers provide less help, e.g. in white-fronted bee-eaters *Merops bullockoides* (Emlen and Wrege 1988) and paper wasps *Polistes dominulus* (Queller et al. 2000; but see Leadbeater et al. 2010). Secondly, the cost of helping may vary, for example according to the helper's chances of obtaining direct fitness benefits in the future, as observed in subordinate foundresses in the social wasps *P. dominulus* (Cant and Field 2001) and *Liostenogaster flavolineata* (Field et al. 2006), and subordinate banded mongooses *Mungos mungo* (Cant 2003). In addition, helpers may withhold help if doing so yields a net fitness benefit, as in the cases of "false feeding" in white-winged choughs *Corcorax melanorhamphos* (Boland et al. 1997), carrion crows *Corvus corone corone* (Canestrari et al. 2004), and meerkats (Clutton-Brock et al. 2005). In this way, helpers may gain indirect fitness benefits from helping but also have the potential to gain direct fitness benefits from not helping. There is thus a tradeoff between investing in direct and indirect fitness benefits, which sets up a volunteer's dilemma (Archetti 2009): a helper does best if someone else helps, but everyone does worse if no-one helps. This in turn may provide selection pressure for others to pay attention to which individuals are helping (Doutrelant and Covas 2007), and subsequently ensure that there is compensation for reduced help, as in long-tailed tits *Aegithalos caudatus* (Hatchwell 1999), or that the "lazy" helper is forced to work harder, as in naked mole-rats *Heterocephalus glaber* (Reeve 1992); however, there is relatively scarce evidence from non-human animals that punishment is used to promote future cooperation (Raihani et al. 2012).

In this study, we use the primitively eusocial paper wasp *Polistes dominulus* to investigate whether group members pay attention to workers' investment in work; that is, the effort they put into foraging for food to feed the queen's offspring. *Polistes* is a genus of primitively eusocial paper wasps, and is a model system for the study of cooperation and conflict (Reeve 1991; Reeve

2001; Field and Cant 2006). Nests are founded by one or many queens, and reproductive skew is high in multiple foundress associations. Subordinate foundresses and, later in the season, workers help rear the dominant's offspring by provisioning larvae. Foraging is costly for *Polistes* workers (Strassmann 1985; Pratte 1989; Reeve 1991), as is the case for other social insects (Schmid-Hempel and Wolf 1988; O'Donnell and Jeanne 1992), and thus is a good measure of cooperation in this system. Although this cost may be counterbalanced by the indirect fitness benefits of helping relatives, some *P. dominulus* nests may include unrelated group members (Queller et al. 2000; Zanette and Field 2008). Additionally, both subordinate foundresses and workers may also have the opportunity to gain direct fitness benefits. Subordinate foundresses can do so by queuing to inherit the alpha position (Leadbeater et al. 2011), and forage less when they have a higher probability of inheritance (Cant and Field 2001); they may also adopt an alternative reproductive strategy of "sitting-and-waiting" to take over other nests (Starks 1998). *Polistes* workers can gain direct benefits not only by laying male eggs, as can other hymenopteran workers (Hammond and Keller 2004), but also by attempting to become foundresses the next year (Reeve et al. 1998); those who adopt this strategy spend more time inactive and less time foraging (Tibbetts 2007).

Polistes is also a model genus for the study of kin, nestmate and individual recognition (Gamboa et al. 1986; Gamboa 2004; Tibbetts and Dale 2007). *Polistes* wasps use cuticular hydrocarbons and nest odors to distinguish between nestmates and non-nestmates (Pfennig et al. 1983; Starks et al. 1998); in addition, species with more complex social systems have individually distinctive facial markings (Tibbetts 2004), and some of these species are able to remember individual conspecifics' faces (*P. fuscatus*: Sheehan and Tibbetts 2008). Our study species, *P. dominulus*,

has variable facial markings that are thought to indicate dominance in North American populations (Tibbetts and Dale 2004; Green and Field 2011); worker and gyne markings differ but overlap (Tibbetts 2006). *P. dominulus* is not thought to be capable of individual recognition in the context of aggression among foundresses (Sheehan and Tibbetts 2010), although there have been no explicit tests of individual recognition among foraging workers. The context-dependent ability of *P. dominulus* workers to discriminate between conspecifics, such as nestmates versus non-nestmates (Starks et al. 1998), makes it reasonable to suggest that workers may be able to keep track of what nestmates are doing, which is a key assumption in this study.

In our experimental manipulation, we removed *P. dominulus* workers for different amounts of time during busy foraging periods, and gave them either access to food or no food while they were kept in the laboratory. We observed each focal removed worker's return to her nest in order to determine whether the time she was away from her nest or whether she had access to food resulted in changes in aggressive behavior after she came back to her nest. Firstly, we consider non-mutually exclusive alternative hypotheses for the potential effect of removing the focal worker for different amounts of time (summarized in Table 5.1a):

Hypothesis 1: time not perceived. Nestmates do not or cannot tell how long a given worker has spent off the nest. *Prediction:* there will be no difference between the aggression received by focal removed worker and that received by any non-focal worker on the nest, regardless of the duration of the focal worker's removal.

Hypothesis 2: lab odor. Nestmates detect a different odor on focal workers who have spent time in lab containers. *Prediction:* the longer a focal spends in the lab, the stronger the odor, and the more aggression she receives relative to non-focal workers.

Hypothesis 3: selfish time away. Nestmates perceive a focal worker spending time off the nest as her selfishly investigating opportunities for abandoning her natal nest. *Prediction:* the longer a focal spends away, the more aggression she receives relative to non-focal workers.

Hypothesis 4: cooperative time away. Nestmates perceive a focal worker spending time off the nest as her cooperatively foraging for food to bring back to the nest. *Prediction:* the longer a focal spends away, the less aggression she receives relative to non-focal workers.

Hypothesis 5: slow foraging. Nestmates regulate foraging based on the rate of incoming wasps, and aggression may be used to activate foraging, as in other social wasps (O'Donnell 1998; O'Donnell 2006; Lamba et al. 2008). *Prediction:* the longer a focal spends away, the more aggression there will be on the nest, but there will be no difference in aggression towards the focal worker relative to non-focal workers.

Secondly, we consider non-mutually exclusive alternative hypotheses for the potential effect of giving the focal worker access to food in the lab (summarized in Table 5.1b):

Hypothesis 6: food not perceived. Nestmates do not or cannot perceive whether a focal worker has had access to food in the lab. *Prediction:* there will be no difference between the aggression received by focal removed worker and that received by any non-focal worker on the nest, regardless of the experimental food treatment. (Note that a wasp potentially paying attention to a worker bringing in food is qualitatively different to a wasp potentially paying attention to whether a particular individual has spent a certain amount of time off the nest, and thus we present hypotheses 1 and 6 separately.)

Hypothesis 7: punishment for laziness. Aggression is used to punish wasps who return from foraging trips without food. *Prediction:* focal workers who have not had access to food in the lab

will receive more aggression relative to non-focal workers than will focal workers who have had access to food.

Hypothesis 8: punishment for eating. Aggression is used to punish wasps who have eaten food before they have returned to the nest. *Prediction:* focal workers who have had access to food in the lab will receive more aggression relative to non-focal workers than will focal workers who have not had access to food.

Hypothesis 9: obtaining food. Aggression is used to take food from wasps who are returning to the nest. *Prediction:* focal workers who have had access to food in the lab will receive more aggression relative to non-focal workers than will focal workers who have not had access to food

Hypothesis 10: insufficient foraging. A focal worker returning having not had access to food from the lab is a cue that other nestmates should increase their foraging rate, and aggression may be used to activate foraging. *Prediction:* there will be more aggression on the nest when the focal returns without food, but there will be no difference in aggression towards the focal worker relative to non-focal workers.

We conducted the experimental worker removals in order to attempt to falsify each hypothesis.

Table 5.1. Summary of hypotheses and predictions relating to (a) the time the focal worker spends off the nest, and (b) whether she had access to food while she was in the lab. "Relative aggression to focal" is the difference between the rate of aggression directed to the focal worker and the mean rate of aggression directed towards any one of her worker-nestmates (this provides an internal control for the background level of aggression on each nest: see methods for more details).

(a)	**Predicted change in aggression with increased focal worker time away**		
Hypothesis	Relative aggression to focal increases	Relative aggression to focal decreases	Relative aggression to focal does not change
1. Time not perceived			√
2. Lab odor	√		
3. Selfish time away	√		
4. Cooperative time away		√	
5. Slow foraging			√

(b)	**Predicted change in aggression with focal worker having access to food (F) versus no food (N)**		
Hypothesis	Relative aggression to focal increases	Relative aggression to focal decreases	Relative aggression to focal does not change
6. Food not perceived			√
7. Punishment for laziness		√	
8. Punishment for eating	√		
9. Obtaining food	√		
10. Insufficient foraging			√

METHODS

Experimental procedure

We conducted a total of 71 removal experiments on 34 *Polistes dominulus* nests naturally occurring on the eaves of buildings at the Liddell Field Station near Ithaca, NY. All nests were in the worker phase (late June – July 2010), and foundresses had been marked earlier in the season before workers emerged. We carried out experiments between 10am and 4 pm on sunny days (temperature 17.3 – 28.1^{o}C), when foraging rates were high.

For each removal, the experimenter used an insect net to catch a worker as she was arriving at or leaving the nest, gave the focal worker a unique mark with dots of enamel paint on her thorax, and put her in a plastic container in the laboratory. Each experimental trial varied with respect to (1) the amount of time the focal worker was kept in the lab, ranging from 8 to 150 min; and (2) whether the focal worker had access to food (F treatment) or not (N treatment), with focal workers in the F treatment having access to a sugar cube and piece of caterpillar (*Manduca sexta* larva) in their containers. We assigned nests to the different food and time treatments randomly with respect to size and location. When we carried out more than one removal on the same nest, we used a different focal worker each time, carried out one F and one N food treatment (counterbalanced for order among nests), and attempted to match the two removals for the time the focal worker was held in the lab. We verified with a χ^2 test that the proportion of wasps caught when arriving, leaving or unknown did not differ between F and N treatments (p>0.2).

After the assigned period in the lab, the experimenter released the focal worker underneath her nest, and immediately began a video recording of the nest. We measured the time the focal worker took to return to her nest after she was released, as she frequently did not fly back to her nest immediately, and captured her return on video. We excluded any experiments that failed (for example, when wasps did not come back, or returned to a different nest), and were thus left with a total of 50 removals from 31 nests; 18 of these nests had focal workers in both an F and an N treatment.

Observations and analyses

We used the video recordings to observe behavior on each nest for the minute immediately after the focal returned. (Pilot observations suggested that there were no changes in behavior associated with the focal's arrival after one minute.) The observer scored the number of aggressive acts (darts and lunges; no other aggressive behaviors were observed, as expected in the worker phase: Reeve 1991) directed towards the focal worker and towards each other worker by both workers and foundresses; all instances of trophallaxis, noting whether the focal or other workers were involved; and the number of other workers (excluding the focal) and foundresses on the nest at the start and end of the observation minute. The observer did not score behaviors when the focal worker was not visible, for example if she went behind the nest during the observation minute, or left the nest before the minute had ended. We controlled for the length of the observation period by calculating rates of aggression and trophallaxis (i.e. instances of aggression or trophallaxis per minute).

We calculated the mean rate of aggression directed towards non-focal workers (i.e. aggression rate divided by the mean number of non-focal workers), and the rate of aggression towards the focal worker. We then subtracted the former from the latter to give the difference between the rate of aggression to the focal and the mean rate of aggression to any other worker on the nest (hereafter, "relative aggression to focal"). We calculated an equivalent measure for the difference between the rate of trophallaxis involving the focal worker and the rate of trophallaxis involving any non-focal worker (hereafter, "relative focal trophallaxis"). Using these measurements provides an internal control for each nest: although external factors such as temperature may affect the rate of *P. dominulus* behaviors (Tibbetts and Reeve 2000), the difference between the rate of the focal's and the mean rate of other wasps' behaviors should not be affected. We verified this in our bootstrap analysis (see below), and subsequently excluded temperature from all analyses. We also checked that relative aggression to the focal worker did not differ among those that were caught when they were arriving, leaving, or unknown (Kruskal-Wallis test: $p>0.4$).

Statistics

The data were not normally distributed, and therefore we used tests that required no assumptions of normality. Firstly, we carried out bootstrap analyses (Mooney and Duval 1993) in Mathematica 8.0 (Wolfram Research), sampling the data 20,000 times. In each bootstrap iteration, the program only took one data set from each nest: that is, it randomly chose data from only one experiment for any nest used for two experiments. This gave 31 data sets for each iteration, and allowed us to exclude nest identity from the analysis. The algorithm generated a

mean value and 95% confidence intervals for the coefficient of each predictor; if the confidence intervals excluded zero, then we consider that predictor term to significantly affect the response term in the model.

Secondly, for the 18 nests used in both F and N treatments, we carried out paired Wilcoxon signed rank tests in R 2.15 (R Development Core Team). This allowed us a more sensitive test of the effect of food treatment.

RESULTS

Effects of time away from nest and food treatment on aggression

In a bootstrap analysis (20,000 iterations, sampling from 31 nests and taking one data set per nest), neither the total time a focal worker spent away from the nest during the experiment, the lab food treatment (food, F; or no food, N), nor the interaction between time and food significantly predicted the relative aggression rate towards the focal worker upon her return (Figure 5.1a). However, in a paired comparison of the 18 nests used in both F and N treatments, relative aggression to the focal was significantly higher in F than in N treatments (Wilcoxon signed rank test: $V = 132$, $p = 0.0092$); that is, the focal worker received more aggression relative to others when she returned with food. Furthermore, relative aggression towards the focal was significantly different from zero in F treatments (one-sample Wilcoxon rank sum test: $V = 178$, $p = 0.0068$), but not in N treatments ($V = 56$, $p = 0.3437$). Thus, when the focal worker had access

to food in the lab, she received more aggression than when she did not have access to food, and also received more aggression on average than did other workers on her nest (Figure 5.1b). Note that our video observations did not confirm whether wasps had fed, as only one focal worker was identified as bringing back food, and we could not determine whether focal workers had food in their crops; however, we did observe workers in the F treatment eating while they were in the lab (J.L. Barker, personal observation).

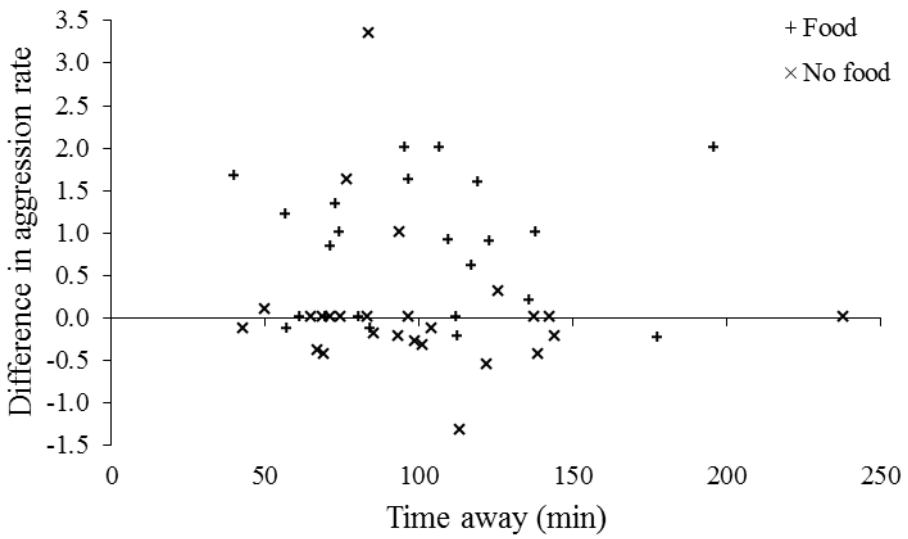
Effects of lab manipulations on time taken to return to nest

In the bootstrap analysis above, we used the total time a focal worker was away from the nest (i.e. time held in lab plus time taken to return after release), because this is what other wasps would perceive if they are paying attention to her absence. However, released focal workers took variable amounts of time to return to their nests. Using the same bootstrap algorithm as above (20,000 iterations, sampling from 31 nests, and randomly taking only one data set per nest for nests used for two experiments) we found that the time the focal took to return to her nest was not significantly predicted by the time she was held in the lab, the food treatment, or the interaction between lab time and food.

Links between trophallaxis and aggression

It is possible that the effect of the experimental food treatment on the relative rate of aggression received by the focal worker is mediated by trophallaxis. Firstly, we included trophallaxis as a predictor in the bootstrap model of aggression, and found that the focal's relative trophallaxis

(a)



(b)

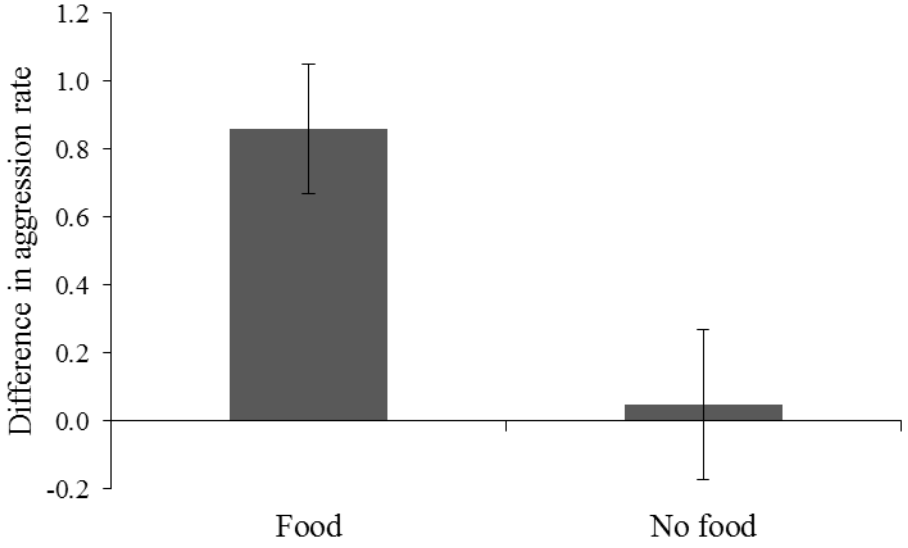
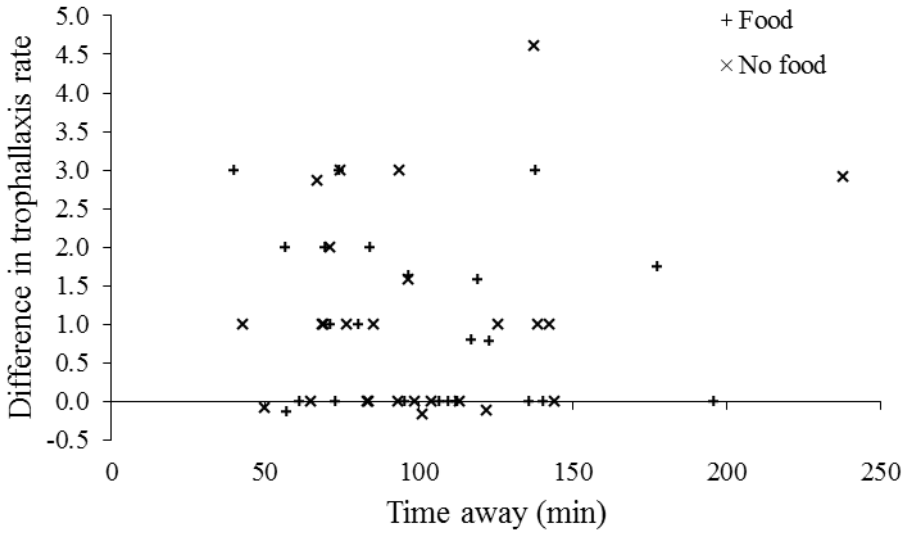


Figure 5.1 (a) The difference between the rate of aggression to the focal worker and the mean rate to other workers was not significantly affected by the time the focal spent away from the nest, whether she was fed, or the interaction between food and time (bootstrap analysis with 20,000 runs, sampling 50 experiments on 31 nests). (b) On the 18 nests on which we carried out both a food (F) and no food (N) experiment, the difference between the rate of aggression to the focal worker and the mean rate to other workers was significantly greater than zero when the focal worker had access to food in the lab, but not significant when she did not (means ±s.e.). This difference in aggression was significantly higher when the focal worker had access to food compared to when she had no food.

rate did not significantly affect the relative aggression she received. Secondly, we carried out an analogous bootstrap analysis of trophallaxis, including time and food as predictor variables in the model, as above, but substituting relative trophallaxis rate for relative aggression rate. In this analysis, neither the time the focal spent away from the nest, the food treatment, nor the interaction between time and food significantly predicted her relative trophallaxis rate (Figure 5.2a). Thirdly, in a paired comparison of nests used in both F and N experiments, food treatment did not significantly affect the focal's relative trophallaxis rate (Wilcoxon signed rank test: $V = 36.5$, $p = 0.5523$); additionally, there was no significant difference between the number of F versus N experiments in which the focal worker engaged in trophallaxis ($\chi^2 = 0.0611$, $p = 0.8048$). However, the focal's relative trophallaxis rate was significantly different from zero in both F treatments (one-sample Wilcoxon rank sum test: $V = 104$, $p = 0.0013$) and N treatments ($V = 135$, $p = 0.0005$). That is, the focal worker engaged in trophallaxis more frequently on average than did other workers on her nest, regardless of whether she had had access to food (Figure 5.2b).

A potential explanation for the increased aggression received by focal workers in the F treatment is that they had consumed food while off the nest but were withholding it from other workers by not engaging in trophallaxis. If this were the case, one might expect relative aggression to the focal to be different between F and N treatments when the focal engaged in trophallaxis, but not in cases when the focal did not engage in trophallaxis, because the workers would not be able to tell whether she had eaten. In fact, in experiments in which the focal was involved in trophallaxis, the relative aggression rate towards her was higher in F treatments than N treatments (insufficient sample size for paired comparison; Wilcoxon rank sum test on 13 F

(a)



(b)

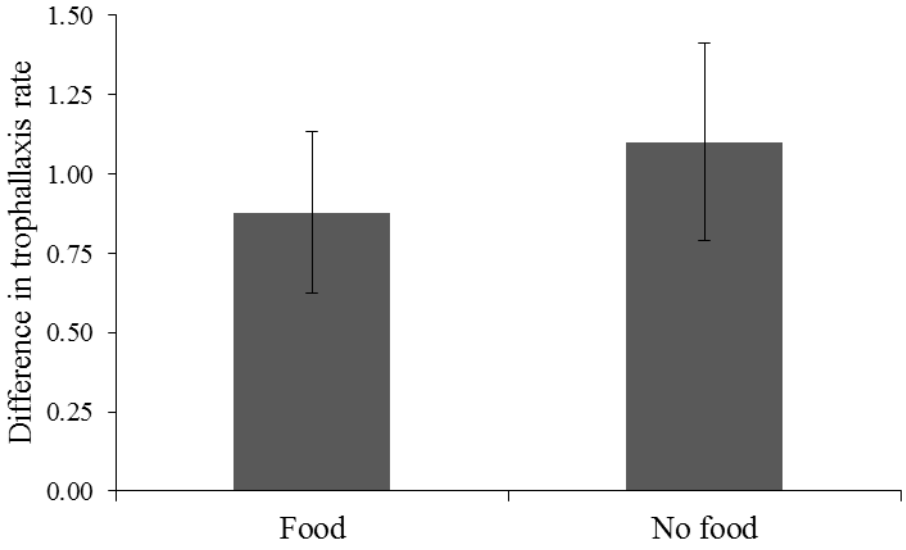


Figure 5.2. (a) The difference between the focal worker's trophallaxis rate and the mean rate of other workers was not significantly affected by the time the focal spent off the nest, whether she was fed, or the interaction between food and time (bootstrap analysis with 20,000 runs, sampling 50 experiments on 31 nests). (b) On the 18 nests on which we carried out both a food (F) and no food (N) experiment, the difference between the focal worker's trophallaxis rate and the mean rate of other workers on the same nest was significantly greater than zero, but was not significantly different between the F and N treatments (means ±s.e.).

experiments and 15 N experiments: $W = 148.5$, $p = 0.0179$; Figure 5.3). In experiments in which the focal was not involved with trophallaxis, this difference was no longer significant (insufficient sample size for paired comparison; Wilcoxon rank sum test on 11 F experiments and 11 N experiments: $W = 87.5$, $p = 0.0805$). Thus, when the focal worker engaged in trophallaxis, she still received more aggression in the F than the N treatment, but this was not the case when she did not engage in trophallaxis.

Effect of aggression on latency to next departure

If a possible function of aggression is to punish focal workers who returned without food, then one might predict that focal workers who received more aggression relative to their nestmates would depart sooner for another foraging trip. In order to test this prediction, we calculated the amount of time the focal wasp spent on her nest after the minute of observation as a percentage of the total amount of time remaining on the video tape after the observation minute. Using the bootstrap algorithm described above, we found that the percentage of time a focal wasp spent on the nest was not significantly predicted by the amount of aggression she received, or by whether she had had access to food in the lab.

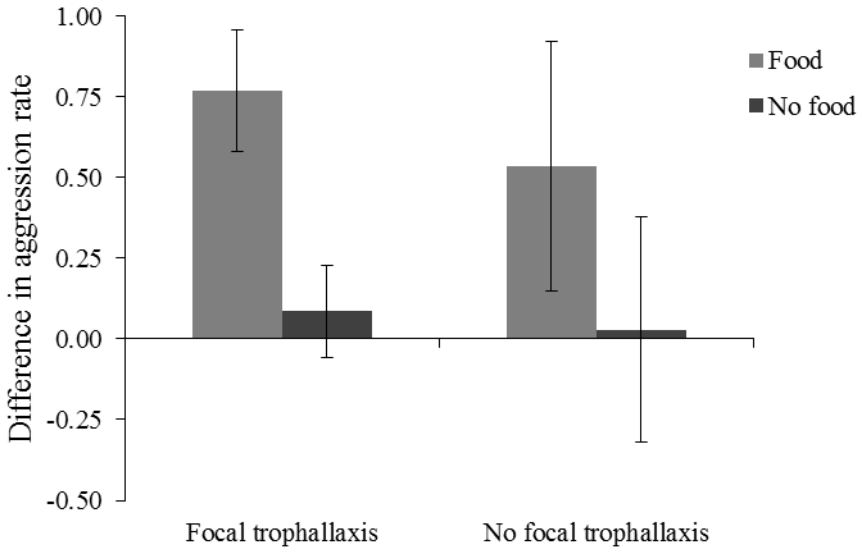


Figure 5.3. In experiments where the focal worker was involved in trophallaxis upon her return to the nest, the difference between the rate of aggression towards her and the mean rate towards other wasps was significantly higher when she had access to food in the lab (*n*=13) than when she did not (*n*=15). When the focal worker was not involved in trophallaxis, the aggression rate was not significantly different in food (*n*=11) versus no food (*n*=11) treatments. Figure shows means ±s.e.

DISCUSSION

Aggression towards returning foragers

For the 18 pairs of nests with one food and one non-food treatment each, focal workers who returned to the nest having had access to food received more aggression relative to other workers than when they returned without having had access to food. This suggests that nestmates are able to perceive some difference in the focal worker, and thus does not support hypothesis 6 (hypotheses and predictions summarized in Table 5.1). This result is also inconsistent with hypothesis 7, which predicts that focal workers receive more aggression when they have not had access to food, as punishment for not bringing food back.

Both hypotheses 8 and 9 predict that focal workers who return to the nest having had access to food would receive more aggression than those who have not, and this prediction is supported by our experimental manipulation of food. The difference between these two hypotheses is in the function of aggression: under hypothesis 8, aggression is a mechanism to obtain food from a focal worker who may be attempting to withhold it, while under hypothesis 9, aggression is a means to punish a focal worker who has eaten food (e.g. it is present in her crop) before she has returned to the nest. If the latter were true, one might expect wasps who received more aggression to depart for another foraging trip more quickly; however, in the bootstrap analysis of the percentage of time spent on the nest after arrival, the relative aggression rate towards the focal worker did not predict how soon she would depart. An additional possibility is that a wasp

who has fed off the nest and received aggression is less likely to do so the next time she forages, regardless of how quickly she leaves.

Although workers in the food treatment did eat while they were in the lab (J.L. Barker, personal observation), we were unable to identify on the video recordings whether focal workers returned with food. Instead, we statistically investigated whether relative aggression to the focal worker in the food versus no food treatment was different when the focal had engaged in trophallaxis upon her return to the nest: if aggression is used to obtain food forcibly, then a worker who engages in trophallaxis may be subject to less aggression. However, the trophallaxis results did not allow us to distinguish between these hypotheses, as the increased aggression towards focal workers who had had access to food in the lab did not differ between instances when the focal worker was involved in trophallaxis and those where she was not. Thus, although aggression may be a means to obtain food forcibly from an arriving forager (hypothesis 8), it is unlikely that wasps are using trophallaxis to mediate aggressive interactions relating to food.

Aggression and regulation of work in wasps and other animals

The results from the paired comparison of aggression in the food treatment are also inconsistent with hypothesis 10, which predicts no difference in relative aggression towards the focal wasp, regardless of food treatment, but rather a decrease in the aggression rate overall when a focal wasp has had access to food. We cannot determine whether the latter was the case using the data presented here, as this study did not include baseline measurements of aggression on unmanipulated nests.

The bootstrap analysis showed that the difference in aggression received by focal workers relative to other workers on the nest was not affected by the total length of time a focal worker spent off the nest. This falsifies hypotheses 2 and 3, which predict that a focal worker will receive more aggression relative to her nestmates when she is away for longer, as well as hypothesis 4, which predicts the opposite effect. This result therefore cannot falsify hypothesis 1: that is, workers do not keep track of foraging effort by different individuals. However, it also does not falsify hypothesis 5: a focal worker spending a longer period of time off the nest may contribute to a slower foraging rate overall, and thus the aggression rate towards both the focal and non-focal workers may increase, in order to stimulate more foraging. This is the case in several other social wasp species, such as *Ropalidia marginata* (Bruyndonckx et al. 2006), *Polistes instabilis* (O'Donnell 1998; Molina and O'Donnell 2009)and *Polybia occidentalis* (O'Donnell 2006). An alternative explanation is that aggression is used to stimulate nest activity, as it is in *Polistes fuscatus* (Sumana and Starks 2004), and as may be necessary when food is brought in after an absence and must be distributed among larvae. However, we cannot address this possibility fully in this study without measurements of aggression on unmanipulated nests.

In sum, combining the analyses of relative aggression towards the focal worker and aggression towards non-focal workers, the results are consistent with more than one of the non-mutually exclusive hypotheses (Table 5.1). Aggression may have a dual function: alerting wasps already on the nest to changes in food flow into the colony, while also being directed towards the incoming forager, dependent on the time she has been away and possible food she has consumed or brought back. Thus, *P. dominulus* workers may keep track of work effort both at the colony level (regulating foraging rate) and individual level (targeting particular incoming foragers based

on their behavior); note that the latter does not require individual recognition, but rather that workers are able to assess cues of nestmates' foraging efforts.

In cases where the colony-level explanation applies, keeping track of work effort may be an important component of the self-organization of many social groups (Gordon 1996; Bonabeau et al. 1997; Fewell 2003). In cases where individual-level behavior is important, the stage is set for potential conflict over different parties' work investments to be translated into actual conflict (Ratnieks and Reeve 1992). Evidence from cooperatively breeding taxa suggests that this may occur in different ways: for example, inactive naked mole-rats receive more shoves from the queen (Reeve 1992) and respond by increasing their work rate; removed helpers in the cooperatively breeding cichlid *Neolamprologus pulcher* were not punished, but increased helping and appeasement behaviors when they returned, perhaps pre-empting punishment (Bergmüller and Taborsky 2005). In contrast, carrion crows appear to tolerate "lazy" helpers, which may provide a buffer for unpredictable scenarios when extra help is needed (Baglione et al. 2010). Thus, two general predictions arise concerning the function of aggression as punishment: firstly, if aggression does act as punishment, then it should be costly to the punished worker; and secondly, "lazy" workers are more likely to be punished when the cost of laziness to any other worker is higher, analogous to hymenopteran worker policing of male production (Wenseleers et al. 2004). Future studies could use a game theoretic approach, e.g. "tug-of-war" models (Reeve et al. 1998), to predict evolutionarily stable investments both in conflict over work and in work itself, and to guide future experimental tests. One might predict conflicts of interest over work effort to arise more frequently in societies where non-breeders have the potential to gain direct fitness benefits (Cant and Field 2001; Field and Cant 2009), although

these conflicts may be suppressed, given the accompanying selection for conflict reduction mechanisms (Ratnieks and Reeve 1992; Frank 2003; Ratnieks et al. 2006). These predictions apply not only to social wasps, but may help shed light on general principles of conflict reduction across social taxa (Reeve 2001).

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